PLANT - HERBIVORE DYNAMICS IN THE BIRUNGAS.

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ABSTRACT

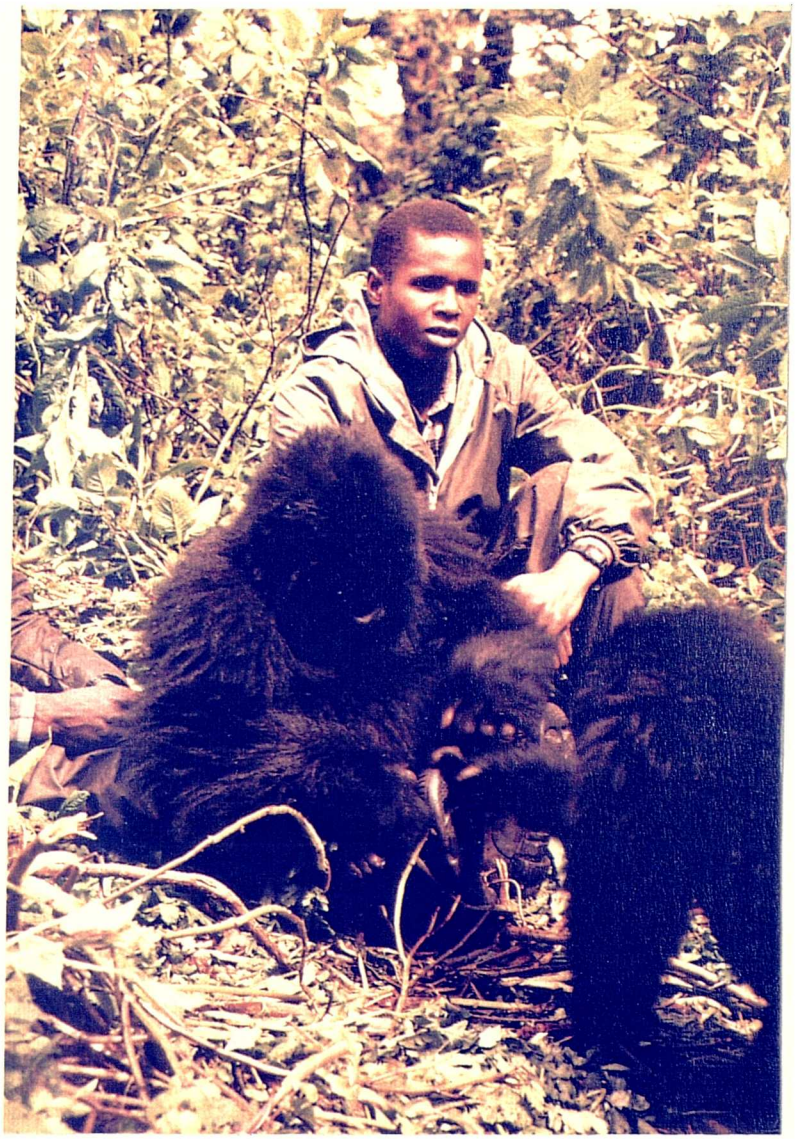
This thesis investigated the plant-herbivore dynamics in the Birungas volcanos in central Africa. The work concentrated on the impact the five largest mammalian herbivores had on the vegetation and the effects this had on the population of mountain gorillas (*Gorilla gorilla beringei*) in this reserve. The work contained here also made a start at providing information about the ecological processes, important in the functioning of this tropical montane ecosystem.

A literature review of ecosystem studies in the tropics highlights the importance of niche separation in the coexistence of species and provides examples of the types of ecological processes that have been found to be important in savannas and forests. It also emphasises the importance of basing park management decisions on studies of the whole ecosystem rather than selected animals. A study of the biomass of plant species in the selected study area showed a patchiness in their distribution, not only in the habitat types which are determined by altitude, but within a habitat as well. Faecal counting methods were used to determine the population size of the selected herbivores and their relative use of each habitat type. These showed that the Birungas supported a relatively high biomass of large mammals compared with other forest ecosystems.

Dietary analysis based on microhistological analysis of faeces and a nutritional analysis of the food-plant species showed that most plant species could provide the nutrient requirements of the herbivores. Therefore there was no evidence for nutrient limitation of populations in this ecosystem as found in studies elsewhere. Analyses of the damage done by the largest herbivores to the vegetation and its subsequent regeneration showed that this had little effect on the biomass of food-plants available to the herbivores. Niche overlap studies showed an unusually high degree of overlap in habitat use but an unusually low degree of overlap in the diets of these herbivores.

A model incorporating the data provided from this study was used to analyse the effects that one herbivore might have on another, particularly on the mountain gorilla. This showed that the elephant population was most likely to affect the food supply of the gorillas, however their population was so low that they were unlikely to be having much impact. The model also indicated that the buffalo and bushbuck were nearer their ecological carrying capacity than the gorillas or elephants.

DEDICATION



I would like to dedicate this thesis to Uwimana Fidele whose hard work, interest and enthusiasm made the data collection so much easier. Africa could do with many more people of his calibre working in its parks.

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There are many people I would like to thank for their help and advice during the three and a half years I have been working on this thesis.

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Résumé

Cette thèse examine la dynamique entre plantes et herbivores dans les volcans des Birunga en Afrique centrale. Le travail mesure l'impact de cinq grands herbivores sur la végétation, ainsique sur leurs consequences sur la population des gorilles de montagne (*Gorilla gorilla beringei*) dans cette réserve naturelle.

Le premier chapitre est un résumé de la littérature scientifique et se concentre sur les études des écosystèmes tropicaux. Il souligne que la gestion d'un parc doit être fondée sur l'étude des écosystèmes plutot que sur l'étude de l'écologie d'animaux spécifiques.

Le chapitre deux fait état d'une étude des biomasses des plantes et montre que la distribution des espèces est inégale, non seulement entre les habitats mais aussi au sein des habitats. Ces distributions augmentent le nombre des niches qui peuvent être utilisé par les herbivores.

Le troisième chapitre présente les résultats du décompte des fèces, qui est une méthode utilisée pour le recensement des herbivores. Les données montrent que les buffles et les guib-harnachés dominent la biomasse des herbivores, et la densité de la biomasse (31Kg/Hectare) est grande pour une foret. Chaque herbivore montre une préférence pour des habitats différents.

Le chapitre quatre est une étude de l'alimentation des herbivores. Les plantes trouvées dans les fèces étaient mesurées en utilisant les cuticules des feuilles pour leur identification. Les éléments nutritifs trouvés dans les feuilles des plantes montrent qu'il y a suffisamment de chaque élément dans presque chaque espèce de plante pour les herbivores. Par conséquent les populations d'herbivores ne sont pas limitées par ces éléments nutritifs.

La productivité des plantes est mesurée dans le chapitre cinq. Les herbivores foulent les plantes et la surface rasée chaque jour par les gorilles, les éléphants et les buffles est mesurée grace a la regénération de cette végétation. La vitesse de la regénération de la végétation rasée par les gorilles et les buffles est presque identique, mais elle est plus lente pour celle rasée par les éléphants.

Le chevauchement des niches des herbivores est mesuré dans le chapitre six et est comparé avec le chevauchement attendu. Ils montrent que la plupart des herbivores sont concentré dans les habitats situés entre les volcans, mais que leur alimentation est plus distincte que ce que les chevauchements attendu. Ces résultats seraient ceux attendus si la compétition existaient entre les herbivores, mais ne prouvent pas que les herbivores soient effectivement en compétition.

Une simulation par ordinateur utilisant les mesures des chapitres 2 à 5 montre que les éléphants pourraient avoir le plus grand impact sur les gorilles de montagne. Cependant, pour le moment, leur nombre est fort peu nombreux dans le parc et ils ne posent pas un problème. Cette simulation montre aussi que les buffles et les guib-harnachés sont près de leur population maximum, mais que les gorilles, les cephalophes et les éléphants pourraient augmenter.

Le chapitre 7 avance quelques idées pour la gestion du parc en utilisant les résultats présentés précédemment. Les populations de grands herbivores devraient etre recensées regulièrement par des comptes de fèces afin de mesurer les changements au sein des populations. Les changements dans la végétation devraient aussi être mesurés.

DECLARATION

Researchers at Karisoke were asked to provide information during this study about the habitat in which the gorillas were found each day. Mineral content, cellulose digestibility and ash of all the main plants in this study were determined by an undergraduate student, Charles Baines. With these exceptions, I declare that all the data collection in this thesis was undertaken by myself, with help from a rwandan tracker. All the analyses were performed in Bristol by myself, under the supervision of Dr. S. Harris. No part of this work has been submitted for consideration for any other degree or award.

Andrew John Plumptre.

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CHAPTER ONE

THE COEXISTENCE OF LARGE HERBIVORES IN TROPICAL ECOSYSTEMS

"A 'laissez-faire' approach to the management of nature reserves is obviously indefensible" M.E. Soulé (1987).

1.1 Introduction

The current theories about island biogeography (Diamond 1975, Pickett & Thompson 1975, Soulé, Wilcox & Holtby 1979), when applied to nature reserves, indicate that the size of a protected area is of great importance in the conservation of species, particularly large mammals. The smaller a reserve the faster a species will become extinct through factors such as disease, predation, competition, and stochastic factors such as droughts, floods, fires or genetic drift. Soulé et al. (1979) concluded that even the largest known national parks in east Africa such as Tsavo (20,800 km^2) and the Serengeti-Mara ecosystem (16,300 km^2) could lose thirty percent of their species within 500 years if they were to be preserved rather than actively managed. It is therefore imperative that national parks and reserves are actively managed for conservation purposes. Ruess (1987) argues that if management is to be effective it must be based at the 'ecosystem level' rather than aimed at particular species, because affecting one aspect of the system can profoundly affect other aspects through positive or negative feedback mechanisms.

The Birungas volcanos is an area of about 400km^2 of tropical montane rainforest on the border of Rwanda, Zaire and Uganda which is currently designated as a biosphere reserve. This designation means that its protection is of global importance because of the habitat type and the rare species it contains. The three parks (one for each country)

that make this reserve form one of the last strongholds of the mountain gorilla (*Gorilla gorilla beringei*), containing at least half the world population of this endangered species. Currently there are thought to be three subspecies of gorilla (Groves 1970); the western lowland gorilla (*Gorilla gorilla gorilla*), of which there are about 40,000, the eastern lowland gorilla (*Gorilla gorilla graueri*), of which there are 3-4,000, and the mountain gorilla, of which there are only about 600 individuals (Vedder 1987, T. Butynski pers. comm.). The mountain gorilla only occurs in the Birungas, where there are currently about 310 (unpublished 1989 census), and in the Bwindi forest in Uganda where there are about 300 animals (T. Butynski pers. comm.). However, it is possible these latter animals may be a distinct subspecies (T. Butynski pers. comm.), and if this proves to be the case, the Birungas contain the only population of mountain gorillas.

The Birungas were designated as a national park in 1925, but it was not until the 1960s that a study of the mountain gorilla was attempted (Schaller 1963). This provided a lot of basic data and was followed by a long term field study initiated by Dian Fossey, who established the Karisoke Research Centre in 1967. Karisoke provided a base for many researchers, and resulted in numerous publications on mountain gorilla ecology and behaviour (Harcourt, Stewart & Fossey 1976, Harcourt 1979a, 1979b, Watts 1983, 1984, Vedder 1984). This research on the gorillas around Karisoke continued for over twenty years, and still continues with three study groups that are now very habituated to humans.

However, during this time there have been few studies on other species in the park. In 1985, l'Office Rwandais du Tourisme et des Parcs Nationaux (ORTPN), World Wide Fund for Nature (WWF), International Union for the Conservation of Nature (IUCN) and the Mountain Gorilla Project drew up a management plan for the park highlighting the importance of research on other aspects of the ecology, geology and hydrology within this ecosystem (D'Huart, Von der Becke & Wilson 1985). If this

park is to be managed effectively in order to maintain the current population of mountain gorillas, it is essential that information is collected about the physical and biological processes that are important in the functioning of the whole ecosystem. One of the major pieces of information needed for effective management is about the structure of plant and animal communities in the park and how they interact. There are very few predators in the reserve, the major ones being feral dogs which are shot by park guards on sight. Therefore the herbivore populations are probably at levels high enough to be having a heavy impact on the vegetation. This thesis gives the results of the first study to attempt to investigate the interactions between the plant and herbivore communities in this reserve.

This review will therefore examine the factors that have been found to be important in determining community structure, concentrating particularly on aspects of competition and the concept of the niche. Then the literature on ecosystem studies in the tropics, particularly Africa, will be reviewed, highlighting those processes that have been found to be important in the determination and maintenance of plant and animal communities in savannas and tropical rainforests.

1.2 The structure of communities

The structure of an ecological community is determined by many interrelated factors such as the patterns of resource allocation, the spatial and temporal abundance of species, trophic levels, nutrient cycling, guilds, competition and niche overlap (Giller 1984). It is only when research is carried out on each of these aspects that a picture is built up as to how the ecosystem functions and how each of the species within it coexist.

Many biological studies to date have concentrated on autecological studies (eg. Grimsdell 1969, Douglas-Hamilton 1972, Schaller 1972). However, as May (1981)

points out, it is not easy to extend studies of individual species to multispecies situations because of the proliferation of relevant parameters that must be taken into account. More recently there have been studies looking at the interrelationships of 'guilds' of species, where a 'guild' is defined as an assemblage of species utilising a particular resource or group of resources in a functionally similar manner (Giller 1984). For example, Fleming, Breitwisch & Whitesides (1987) review the ecology of the vertebrate frugivore guild in the Old and New World. They argue that ecological processes have profoundly influenced the evolution of tropical frugivore faunas and communities on each continent, thereby creating more differences than similarities between these communities. It is thought that competition between frugivores in each region could be one of the factors that has led to this divergence.

It is within guilds that competition will occur because the species concerned are all utilising a similar resource. There has been much controversy, however, in the last ten years about the importance of competition and what role it plays in shaping a community (MacNally 1983, Schoener 1983, den Boer 1986, Underwood 1986). Schoener (1983) reviewed the literature on competition and only found about 160 field experiments that demonstrated competition. There have been many more experiments in greenhouses and laboratories such as Park's (1962) work on *Tribolium*, although it can always be argued that these situations are artificial and would not occur in nature.

In the case of herbivores it has been argued that competition should not exist because these animals are not food limited (Hairston, Smith & Slobodkin 1960, Slobodkin, Smith & Hairston 1967). If they were food limited massive defoliation would occur (Belovsky 1983). Schoener (1983) suggested that predation keeps the population of herbivores below a level that can remove enough primary production to create situations where food is limiting. There are good reasons for thinking that competition between species of phytophagous insect is relatively rare because intraspecific

competition appears to be small (Strong, Lawton & Southwood 1984). If organisms do not compete with members of their own species they are likely to compete to a lesser degree with members of another species.

An argument against the theory that herbivores cannot be food limited is that many leaves are not edible because they contain toxins from secondary compounds (Rhoades 1985). In fact for many large herbivores there is good evidence that food limitation does occur (Sinclair 1975, Belovsky 1981), even where there are many predators such as in the Serengeti (Sinclair 1975). For many other regions predators have been virtually wiped out by man and here there must be other factors that regulate the herbivore population. This is most likely to be the food supply, although it has been found that climatic and social factors can also regulate populations (Ohsawa & Dunbar 1984).

If animal populations are limited by a shortage of some resource then competition may occur between species using this resource. It is not true to say that competition will always occur however, because niche theory would predict that each species would alter its use of the resource, thereby reducing the potential for competition.

Grinnell (1917) first coined the term 'niche' and this was expanded by Hutchinson (1957) to produce the current concept of the 'n-dimensional hypervolume'. Each organism can exist within a range of values for any particular resource in the environment. Plotting each of 'n' resources against one another in multidimensional space would produce an 'n-dimensional hypervolume' characteristic of each species.

The 'fundamental niche' describes the entire set of conditions that an organism can inhabit when there is no competition. The 'realised niche' is the set of conditions in which an organism exists in the 'natural world' where predation and competition can restrict its access to certain resource states. If the realised niche for an organism in an

ecosystem is too small to support itself then it will die out or have to migrate to survive. This is the basis of Gause's (1937) competitive exclusion principle, which states that if two competing species coexist in a stable environment, they do so as a result of niche differentiation. Otherwise one species would exclude or eliminate the other. Therefore one would expect some level of differentiation of niche structure when studying guilds of animals and this is generally what is found. Schoener (1974), in his review on competition, found that the separation of animal species on the habitat dimension was the principal method of resource partitioning. Diet was the second most important separating factor, although this may be partly biased by the fact that more studies have looked at these resources than at others.

As an example of this principle, Connell (1961) studied two species of barnacle on a rocky shore. He showed that *Chthamalus stellatus* generally occurred higher up the shore than *Balanus balanoides*. By studying individuals of each species he was able to show that *Balanus* cannot survive the desiccation further up the shore whereas *Chthamalus* can. Lower down the shore *Balanus* competitively excluded *Chthamalus*, thereby reducing the latter's fundamental niche to a smaller realised niche.

Similarly, Putman (1986) showed that large mammalian herbivores in the New Forest partition the available resources between them. For example, although the cattle and ponies had similar diets, they tended to use different habitats within the forest. Even where they did overlap in the use of a particular habitat such as the meadows, there appeared to be spatial separation on a finer scale in the use of these areas. Dietary overlap between cattle and the three species of deer was lower than the ponies and this separation was enhanced even further by the use of different habitats. In this example however, it is not possible to state for certain whether or not this partitioning was due to competition. The niche separation may have been due to physiological or morphological factors. For example, the cattle could not have survived upon the diet eaten by roe deer because their incisor arcade is too broad for selective browsing

(Illius & Gordon 1987) and their rumens have evolved to deal with a roughage diet (Hofmann 1973). It may simply have been that the fundamental niche differed for each of these species and that their realised niche was little different to the fundamental niche.

There are many other examples of studies on habitat use and diets of animals, but I shall not attempt to review them all. In order to understand how these processes play a part in the functioning of a community within an ecosystem, it is necessary to review the available information on the factors that are important in determining the plant and animal communities in the ecosystem itself. A review of studies of other ecosystems in the tropics will therefore show what factors may be important in determining plant species distribution and animal numbers in the Birungas.

1.3 Ecosystems in the Tropics

The tropics are generally richer in species and more diverse than temperate regions, although the reasons for this are not clear. Janzen (1970) proposed that tropical forest communities contain a high number of 'predators' of seeds and seedlings and it is likely that mortality will be higher close to adult plants where the bulk of the seeds will fall. This would encourage a more diverse forest type because seedlings of the same species would be prevented from germinating near the parent plant, thereby allowing other species to fill the gaps. An argument against this, however, is that the high host specific predation is part of the community itself and therefore could not be the root cause for the high species richness in the first place. A more persuasive argument is that richness is related to primary productivity, and this increases from the poles to the tropics. However, increased productivity does not necessarily mean an increase in plant species diversity or richness. There are many examples where increasing nutrient levels in rivers or on land increases the productivity of certain

species relative to others, these plants outcompete the others and actually reduce diversity through eutrophication (Rosenzweig 1971).

Tropical soils tend on average to have lower nutrient concentrations than temperate soils because most nutrients are locked-up in the plant biomass or are leached from the soil by heavy rainfall. Therefore the increased species richness may actually reflect a low productivity where nutrient 'patchiness' supports a more diverse flora. The greater evolutionary age of the tropics may also be a factor that can explain some of the increase in species richness. The repeated fragmentation and coalescence of tropical forest refugia will have allowed greater genetic differentiation and speciation (Connor 1986).

Whatever the cause, the high plant biomass and its primary production can sustain a large biomass of primary and secondary consumers. This is most obvious on the tropical savannas (Delaney & Happold 1979).

1.3.1 Savannas

The savannas in Africa have been one of the most intensively studied ecosystems in the tropics (Sinclair 1975, Sinclair & Norton-Griffiths 1979, Bell 1982, McNaughton 1985, Ruess 1987, McNaughton, Ruess & Seagle 1988) so that many of the factors that govern the plant-herbivore dynamics of these regions are now understood. It is therefore worthwhile reviewing this literature because far less is known about tropical forests.

Censuses show that savannas can support a high biomass of wildlife compared to other environments (Coe, Cumming & Phillipson 1976, Botkin, Mellilo & Wu 1981) and the biomass can be predicted from the amount of rainfall (Coe, Cumming & Phillipson 1976). In the Serengeti many populations of herbivores are limited by

seasonal constraints on the availability of their food supply (Sinclair 1975, 1977, Sinclair, Dublin & Borner 1985). This usually occurs during the dry season when plant productivity is at its lowest (McNaughton 1985). Whilst the potential for competition between the various herbivores is high, this is minimised by a separation between the herbivore species in their use of the available resources.

For example many studies have shown that the herbivores in the savannas utilise the available habitat differently (Ferrar & Walker 1974, Hirst 1975, Leuthold 1978, Boer & Prins 1990). In the Serengeti the migrating herbivores physically alter the habitat as they move, thereby leading to a succession of grazing herbivores, each using a different height of grass as it is steadily removed (Bell 1971). However, the most obvious separation between herbivores, is along the grazer-browser continuum (McNaughton & Georgiadis 1986). In addition there is variation in the species of plant consumed, depending upon the selective ability of the animal concerned (Jarman 1971, Hofmann 1973, McNaughton & Georgiadis 1986). Many ruminants select particular parts of the grasses they consume, avoiding the tough fibrous stems and selecting the more protein-rich leaves (Sinclair 1977, Stanley-Price 1978, McNaughton 1985). It has even been shown that browsers using the same foodplants may reduce the potential for competition by feeding at different heights (du Toit 1990).

Although most studies have emphasised the degree of separation of herbivores within savanna ecosystems, Walker (1979) considered the degree of overlap. He argued that rather than showing differences, the striking feature about most studies is the high degree of overlap between species. The degree of overlap is usually greater than the degree of separation and this he argues allows the animals greater flexibility in their habitat use and diets. This means that any alterations in the structure or composition of the vegetation can be accommodated, allowing a particular species to survive periods of change rather than die out because its requirements are too specialised.

This flexibility allows switching of vegetation components in the diet when certain plants are reduced in abundance.

More recent studies in savannas have concentrated upon the nutrients cycling within the ecosystem. Bell (1984) argues that soil properties and rainfall have the dominant effects on the plant-herbivore interactions, since these factors determine the relative production of the various plant components. High water availability generally favours fibre production over protein production, and high nutrient supply favours protein over fibre production. This separates savannas into various types: moist-oligotrophic savannas tend to have a high biomass of low quality vegetation, whereas arid-eutrophic savannas have a low biomass of high quality vegetation. It is the arid-eutrophic savannas that support the high biomasses of selective grazers and browsers.

Ruess (1987), however, has shown that this system is far less static than I have portrayed so far. Herbivores can modify their environment and may even have the ability to regulate system processes. Herbivore grazing at moderate levels can stimulate grass production (McNaughton 1985) and it has been shown that simulated grazing increases nitrogen uptake from the soil (Ruess, McNaughton & Coughenour 1983). There is therefore a positive feedback mechanism which can actively promote grazing. Through the continual removal of older plant tissues, herbivores prevent nutrients from being locked-up in unpalatable plant material and they maintain a dense nutrient-rich sward (Ruess 1987). Nutrients are recycled rapidly through the deposition of faeces and urine, so that the presence of herbivores increases the rate of cycling. Botkin, Mellilo & Wu (1981) suggest that herbivores concentrate the nutrients at the soil-plant-grazer interface and actually increase the proportion of nutrients in an available form cycling near the soil surface by preventing the loss of nutrients through leaching. McNaughton (1983), however, found a significantly non-random distribution of herbivore dung deposition in the Serengeti, suggesting that herbivores may act as 'nutrient conduits', concentrating nutrients in certain regions.

On a more dramatic scale, large herbivores can exert very obvious effects on savanna ecosystems. In particular, high elephant numbers in a region can reduce the amount of woodland through 'barking' damage and pushing over of trees, thereby increasing the amount of grassland as the habitat is opened up (Laws 1970, Jachmann & Bell 1984, Kortland 1984). Owen-Smith (1987) extends this to extinct 'mega-herbivores' that once existed in the neo-tropics, suggesting that they maintained the habitat as a more open woodland. However, when they were eliminated by human pressure the habitat altered dramatically, thereby causing many of the other extinctions that occurred during the Pleistocene.

Although herbivores can have marked effects on the vegetation in savanna ecosystems, it is still the nutrient status and water supply that determines the existence of the savanna rather than some other biome. Herbivores can only modify the ecosystem to some extent. Where soil water availability is high, fibre production has been shown to be promoted as stated earlier (Bell 1984) and consequently at the highest levels of rainfall the savanna ecosystem is lost altogether and is replaced by forest.

1.3.2 Lowland tropical rainforests

"Tropical rainforest" covers a variety of forest types and therefore is subdivided into several classifications depending upon the amount of rainfall and altitude. In the savannas there is a strong correlation between primary production and evapotranspiration (Rosenzweig 1968), but there is no evidence for this in rainforest (Leigh 1975). Most of the primary production occurs in the canopy around 30 metres above the ground. This precludes the presence of a high biomass of terrestrial mammals, and therefore the density of large herbivores in forests is much lower than on the savannas. However, if the biomass of arboreal herbivores is added to that of the

terrestrial animals, then the total biomass is comparable with those of some savannas (Eisenberg & McKay 1974).

An estimate of primary production in the canopy can be obtained by measuring the amount of leaf fall over a year. On Barro Colorado island in Panama this is of the order of 7000 kg ha^{-1} yr^{-1} (dry weight). Of this, arboreal vertebrates consume about 150kg ha^{-1} yr^{-1} and insect herbivores about another 400kg ha^{-1} yr^{-1} (Leigh 1975). Yet, despite the high levels of rainfall, there is still seasonality in the production both of new leaves and of fruit (Leigh, Rand & Windsor 1982). Hence although primary productivity is high, vertebrate folivores and frugivores are probably limited by the shortage of food at certain times of year (Leigh & Windsor 1982).

The biology of tropical forest mammals is so poorly understood that it is difficult to compare forest and savanna communities (Dubost 1984). There have been some recent studies which have attempted to look at the partitioning of resources by communities of vertebrates, although these are still few in number (Feer 1989). Emmons, Gautier-Hion & Dubost (1983) investigated the distribution of 66 mammalian consumers in lowland rainforest in Gabon. It was found that these animals reduced the amount of potential overlap by using different habitats, living at different heights within the forest, being active at different times of day (which can reduce overlap if the availability of food such as insects varies with time) and by feeding on different food types. Although this was a fairly crude study, it showed that there were about equal numbers of terrestrial and arboreal species, and of nocturnal and diurnal species. However, there were about five times as many frugivores as folivores. This can be explained by the fact that most leaves as they mature develop anti-herbivore defenses such as toxic alkaloids and cyanogens, or tannins and lignins which reduce their digestibility (Rhoades 1985). Therefore most folivores will only eat the young leaves on a plant, and this is why the seasonality of leaf-flush can limit folivore populations (Leigh & Windsor 1982).

A comparison of this work in Gabon with work on the Malayan Peninsula shows a comparable number of primary consumer species and similar folivore/frugivore and arboreal/terrestrial ratios. If these numbers are also compared with temperate forests it is found that much of the increase in diversity of species in the tropical forests is attributable to the increase in frugivorous species (Emmons, Gautier-Hion & Dubost 1983). The frugivorous species in Gabon have a high degree of overlap in their choice of fruit and hence a high potential for competition (Gautier-Hion, Emmons & Dubost 1980) In contrast, terrestrial frugivorous ruminants such as duikers have a low overlap in food choice in the tropics, despite an often high availability of food, suggesting that for these species food is not limiting (Dubost 1984).

As altitude increases rainforests change in stature; at about 2000 meters the canopy is reduced from three layers to one and leaves are smaller in size; above this altitude montane rainforests occur (Leigh 1975).

1.3.3 Montane rainforest

Montane forests show an obvious zonation of vegetation types with a decrease in biomass as altitude increases, although why this should be so is unclear. It may be due to periodic water or nutrient shortage at different altitudes or a consequence of increased exposure to wind (Whitmore 1989). Leigh (1975) suggests that transpiration is blocked when the air is saturated with moisture and when temperatures are low. This would prevent nutrient uptake and consequently restrict the growth of plants. Temperatures also fluctuate widely from high values due to the high radiation in the thin atmosphere down to near freezing at night and this could also play an important role. Grubb (1977) has also suggested that the rate of nutrient cycling may differ with altitude.

Heaney & Proctor (1989) suggest that montane forests are limited by nitrogen availability and possibly also by phosphorus limitation. Healey (1989) showed that relatively more mass is invested in roots in montane environments and by adding nitrogen or phosphorus to the soil foliar growth was increased, indicating that these nutrients are limiting in at least some montane forests.

The montane forests of East Africa are thought to have provided refugia for many rainforest species during glacial periods throughout the Quaternary. Chapman (1983) suggests that at periods of glacial maxima the climate would have been more arid, causing a reduction in the areas of rainforest in Africa. Only those areas receiving high rainfall would have maintained their forests, and this fragmentation of the forests would have encouraged the speciation of the flora and fauna. The Birungas volcanos are thought to have provided one such refuge, along with the Ruwenzori mountains and the Bwindi forest on the western Rift.

1.4 The Birunga Volcanos and the study site

The montane forest that covers the Birungas ranges in altitude from 2,500m to 4,500m and encompasses most of the vegetation zones typical of African mountains. The distinctiveness of each of these vegetation zones makes the study of their use by the different herbivores of interest because it provides one way in which the herbivores in the park might avoid competing with each other.

The area selected for this study was the region around the Karisoke research centre and encompassed all of the major vegetation zones found in the reserve (Figure 1.1). This region was also chosen because it has been described as a rich region for mountain gorillas (Weber & Vedder 1983 - see Figure 1.2). It has also been protected for the longest period from the action of poachers and therefore the animal populations will have had time to approach or reach carrying capacity. The study area

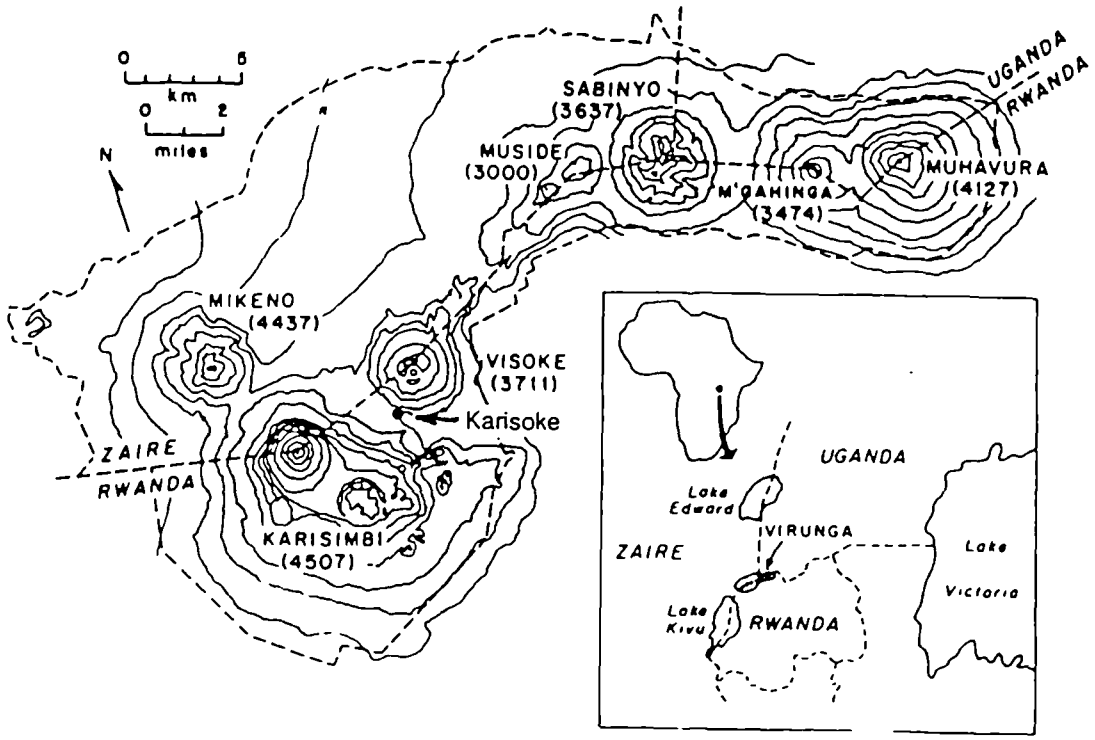


Figure 1.1 The three Birunga conservation areas. Bounded regions include the Parc National des Volcans (Rwanda), Parc des Virunga (Zaire), and the M'Gahinga Conservation area (Uganda). The location of Karisoke is shown. Map taken from Weber & Vedder (1983).

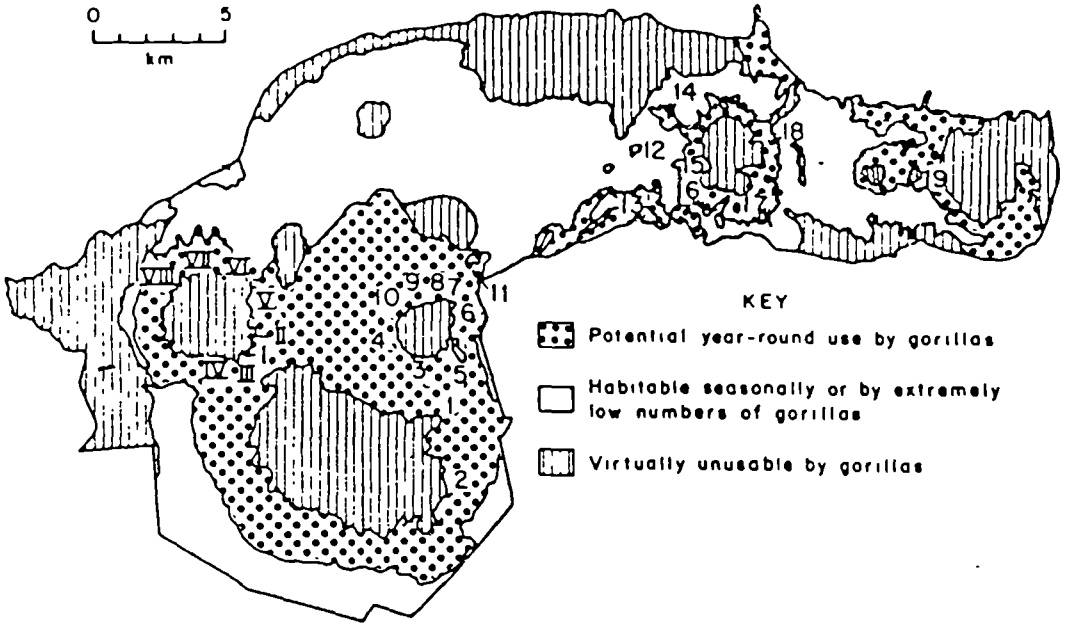


Figure 1.2 The suitability of different areas of the park for supporting mountain gorillas. The numbers refer to different gorilla groups located in the 1976 and 1978 census, and show that the area around Karisoke provides a good habitat for the gorillas. Map taken from Weber & Vedder (1983).

was bounded by the edge of the park in the east, the Suza river in the south and the volcano Bisoke to the north. The southern slopes of Bisoke were included in the study up to a line running east-west across the centre of the crater lake. A line running due south from the western edge of the base of Bisoke formed the western boundary. This meant that the bulk of animal movements into the region would have come from the west because it is unlikely that many animals would have climbed to the summit of Bisoke and down the other side. Deep ravines prevented most movement around the side of the volcano and the ravine in which the Suza river runs limited animal movement to a few crossing points.

Between January 1988 and January 1990 a two year field study of the five largest mammalian herbivores around Karisoke was made in order to provide information about the plant-herbivore dynamics of this region. This was aimed at providing data upon which management decisions could be based in the future. These five herbivores were: the black-fronted duiker (*Cephalophus nigrifrons*), the bushbuck (*Tragelaphus scriptus*), the African buffalo (*Syncerus caffer*), the African elephant (*Loxodonta africana*) and the mountain gorilla (see plates).

The aims of the study were to determine the ways in which these animals use the available resources, the extent of niche overlap between them and the potential for competition, with a view to predicting the impact each herbivore might have on the ecosystem. Ultimately the aims of the park management plans are to encourage an increase in the numbers of mountain gorillas and so it is important to identify whether the impact of these other species upon the environment has a negative effect upon the gorillas.

Black-fronted Duiker
(*Cephalophus nigrifrons*)

Bushbuck
(*Tragelaphus scriptus*)

African Buffalo
(*Syncerus caffer*)

Mountain Gorilla
(*Gorilla gorilla beringei*)

African Elephant
(*Loxodonta africana*)

1.4.1 Thesis outline

Chapter 2 provides a detailed description of the study area, dividing it up into various habitat types. For each habitat the biomass of the available food plants is determined and the plant species distribution related to physical factors in the environment.

Chapter 3 describes how the number of each species of herbivore was determined and how each species uses the available habitats. Herbivore biomass is calculated, related to altitude and compared with other ecosystems.

The diets of each of the herbivores are described in Chapter 4, comparing food selection with availability and gut morphology. Nutrient contents of food plants are measured and related to the observed diets.

Plant productivity is covered in Chapter 5. Seasonal growth rates and the productivity of trampled vegetation after gorilla, buffalo or elephant damage are described and a measure of the rate of trampling damage also obtained.

Chapter 6 synthesizes each of these various lines of research into an analysis of the niche characteristics of each species of herbivore, the degree of niche overlap and the potential for competition between species. The plant-herbivore dynamics of the ecosystem are modelled using the data from Chapters 2 to 5 to predict the effects of an increased density of each species upon the environment.

Chapter 7 summarises the conclusions and relates them to current and future management policies for the park.

CHAPTER TWO

SPATIAL PATTERNS OF PLANT AVAILABILITY

2.1 Introduction.

Pattern in the distribution of plant species occurs in all ecosystems from the gross distinctions of savanna and rainforest at the macro level down to changes in the distribution of individual plant species at the micro level. The causes of any pattern will be due to a variety of factors such as differences in soil nutrient levels, or variations in the macro and micro climate. It is this pattern of plant species within a community that can lead to an increased diversity of animal species. Animals in their turn can alter the vegetation and affect the basic pattern, increasing or decreasing the variation in the distribution of plant species. For example, Cameron (1935) showed that ragwort (*Senecio jacobaea*) will only occur in pastures heavily grazed by cattle or rabbits. Similarly the changes that occur in the vegetation of the Serengeti after the exclusion of animals shows the effect animals can exert upon their ecosystem (McNaughton 1979). The study of pattern in the distribution of plant species is important when investigating herbivore ecology because variation in plant availability will affect the distribution of the animals that feed upon them.

In the Birungas ecosystem pattern at the macro scale has already been identified by various studies (Lebrun 1960a, 1960b, Schaller 1963, Spinage 1972, Fossey & Harcourt 1977). These have shown that there is a clear change in the distribution of plant species with an increase in altitude, and that this forms very distinct habitat types. Marius (1976) mapped 14 different habitat types throughout the park based upon aerial photos. These range from a *Xymalos* - *Dombeya* mountain forest at the lowest altitude, although this has now mostly been cleared for farmland, through bamboo forest and a *Hagenia-Hypericum* woodland, up to the subalpine and alpine

habitats at the top of the volcanos. The altitudinal limits of boundaries between lower and upper montane forest and between upper montane forest and subalpine and alpine habitats have been noted for most mountains in Africa. These limits occur over relatively sharp altitudinal bands, however the altitude at which these bands occur varies with the size of the mountain, being higher on the more massive mountains. This is known as the 'massenerhebung effect' (Leigh 1975, Grubb 1977).

Since there are obvious changes in the vegetation, creating various habitat types, the distribution of plant species between each habitat is likely to vary. As the main aim of this study was to understand the ecology of the major mammalian herbivores, a study of plant species distribution is necessary to understand the availability of food items for each of the herbivores. This in turn may provide some insight into how and why the animals are using each of the habitat types. Biomass was chosen as the measure of availability because it is more meaningful in terms of the animal species ecology than measures such as frequency or density of the plants. If it is assumed that all the food plants measured are edible to the animals as food, then this total biomass can be used to model the maximum number of animals that the ecosystem can support. This assumption is invalid for many tropical forest ecosystems where plants are heavily protected by allelochemicals (Rhoades 1985). In these ecosystems only the youngest leaves are available to the folivores as food. The Birungas ecosystem, however, is dominated by herbs and grasses which are relatively short lived (when compared with woody species) and so would not be expected to invest so much energy in producing such chemicals (Cates & Orians 1975). Watts (1983) analysed many of the herbs eaten by mountain gorillas in the Birungas and found few alkaloids or tannins present, thereby indicating that such an assumption is reasonable in this case. An estimate of the total biomass of food available for each species of herbivore is also important when investigating the potential for competition, since food has to be limiting before any inference can be made about dietary competition.

Multivariate ordination techniques have been developed since the early 1970s to investigate how the structure of plant communities is determined by underlying physical or biological factors (Greig-Smith 1983, Kent & Ballard 1988). These assume that plant species respond to various ecological gradients in different ways, thereby providing some degree of separation along that gradient. The current techniques assume that each plant species has a Gaussian response model (bell-shaped curve) with respect to the gradient and this is what distinguishes these ordination techniques from other multivariate techniques such as principal components analysis (Pielou 1984, Minchin 1987, Ter Braak 1987). However, like principal components analysis, these techniques pull out ordination axes which reduce the variation to single dimensions.

Plotting the first few axes against each other produces two or three dimensional diagrams which express the main variation between plant species distributions (Ter Braak 1988). These axes are constrained to be uncorrelated with each other but they are not necessarily independent of each other (Hill & Gauch 1980). A technique referred to as detrending is employed as a means of making each axis independent of another (Hill & Gauch 1980, Ter Braak 1986). Detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) appear to be the two most commonly used techniques at present for plant ordination. DCA is an indirect gradient analysis which ordinates the plant community and can then correlate the axes obtained with environmental data. CCA on the other hand incorporates the environmental data in the ordination process so that it detects the patterns of variation in the community composition that can be explained best by the environmental variables measured (Ter Braak 1986). Both of these techniques can produce axes in units of compositional turnover or mean standard deviation (SD) of species (Gauch 1982, Økland 1986). If this is done then any two species separated by 4SD along an axis or coenocline are unlikely to be found together in the same plot (Hill & Gauch 1980, Økland 1986). Thus such a technique can be used to investigate pattern at the

individual species level and can be used to produce hypotheses about the causes of this pattern.

2.2 Methodology

Eight habitat types were selected in the study area from those used by Watts (1983) and Fossey & Harcourt (1977) in previous studies. However, certain of their classifications were combined into one habitat where the total area of the habitat was small. For example the nettle zone (Watts 1983) was included with the herbaceous zone due to it being on the fringe of the study area. The habitat classification used was also chosen to ensure that each habitat could be identified from aerial photos. These eight habitat types are as follows:

1. Bamboo
2. Saddle - a *Hagenia-Hypericum* woodland.
3. Meadow - Lower altitude meadows around Karisoke.
4. Herbaceous - areas with no tree canopy and many tall herbs.
5. Brush-Ridge - *Hypericum* woodland on the slopes of Bisoke.
6. Giant *Lobelia* - a region with a high density of *Lobelia stuhlmannii* around 3,400 metres on Bisoke.
7. Alpine - *Senecio johnstonii* interspersed with small meadows at the summit of Bisoke.
8. Karisimbi meadows - High altitude meadows interspersed with *Hypericum* and *Senecio johnstonii* at the base of the volcano Karisimbi.

This last habitat was designated because it was sufficiently different from the Alpine and Giant *Lobelia* zones to be classed as such. It also had much shallower slopes allowing easy access to the area for animals.

Within each of these habitat types a stratified random sampling technique (Greig-Smith 1983) was used to sample the availability of plant species. In the majority of vegetation types a grid with cells of 140 paces square was used, selecting a plot at random within each cell. Some habitats which were relatively small required a smaller grid cell in order to achieve enough samples and for these a cell of 70 paces square was used. The average pace was measured as 70cm giving grid cells of 98m x 98m and 49m x 49m respectively. Pace length was checked regularly using a measuring stick because it could vary on the steep slopes in the study area. A plot would be chosen from 100 possible sites within a cell using random number tables, the front of the last pace marking the centre of the plot. Plants were measured as follows within circles of increasing radius from this central point as follows:

1. $1/10^{th}$ m^2 plot: all small clover-sized herbs and grasses were collected and labelled by species for drying and weighing. Only live green material was collected.
2. $1m^2$ plot: all larger herbs were counted and the height of the main stem measured. *Galium* and the leaves of vines and bamboo were also collected for drying and weighing.
3. $5m^2$ plot: all Giant *Lobelia* and bamboo stems were counted. Lengths of *Hypericum revolutum* and *Rubus* spp. twigs were measured.
4. $10m^2$ plot: all tree species were counted.

All plants collected were cut at ground level although it is realised that this total mass of plant material will not be equally available to each of the herbivores. For instance buffalo cannot feed as close to the ground as duiker and hence the biomass available to buffalo will be less. However, it was felt that this difference compared with the overall biomass would not be very great so that one figure for the mass of available plant material was used. Plant species were identified from herbarium material at Karisoke and from the flora of Rwanda (Troupin 1977-1988), and those identified are

listed in Appendix 1. Plants were dried by a charcoal stove by a Rwandan assistant until there was no further loss in weight. The plants were weighed to the nearest 0.1g. For the larger plants, lengths measured (to the nearest centimetre) were related to dry biomass by harvesting about 40 individuals of different sizes for each species, drying and weighing them to obtain regression equations for total mass and leaf mass. In the case of *Peucedanum linderi* and *Carduus nyassanus* leaf length and stem height were measured separately in the $1m^2$ plots because both of these plants grow as rosettes initially with no stem. If a plant branched greatly then each of the lengths of the separate branches was measured. The leaves of bamboo, and the twigs of *Rubus* and *Hypericum* were only measured within 2m of the ground as there was little sign of animal browsing above this height. An average biomass of *Lobelia giberroa* leaves per plant was obtained by measuring the mass of leaves harvested from 20 plants and obtaining a mean. The stem density of *Lobelia giberroa* obtained in the vegetation survey was then multiplied by this value to obtain the available leaf mass for this plant. Before a plot was harvested the two main plant types were noted in the $1m^2$ plot and a measure of the altitude (to the nearest 25m) and angle of slope taken.

A stratified random sampling technique was employed instead of the system used by Watts (1983) because it allows a calculation of the variance and standard error of the mean. On the slopes of Bisoke it was not always possible to sample every possible grid square due to the difficulty of crossing large ravines; however, since this same problem was also faced when studying the habitat use of the various herbivores (see Chapter 3), the vegetation that was ultimately measured was in the areas where herbivore use was also measured, so that the inability to reach some of the grid squares should have little bearing upon the final analysis.

Climatological data were collected daily at the Karisoke meteorological station throughout the study period. Rain gauges were also placed in most of the habitat types

up Bisoke and down near the edge of the park and these were monitored at weekly intervals by Karisoke staff.

Using a 'Stereopret' (Paine 1981), an orthographic projection map from 1:20,000 scale aerial photos (taken in 1979/1980) was made at the University of Leuven in Belgium. This corrects for the topographic displacement that is found on aerial photos. Each of the eight habitat types was mapped on to this contour map from the photos. The scale of this map varies with altitude, with those regions nearest to the camera appearing larger. Therefore in order to calculate the areas of each habitat type within the study area a separate scale was used for each 50m increase in altitude. Areas were measured using a digitiser over regions where the contour lines were uniformly spaced and then corrected for the degree of slope, given that there was a 50m rise from one contour line to the next. The areas of each small section of the map were then summed to produce the total area of each habitat type.

Ordination of the plant biomass data was performed for each habitat type using the program CANOCO (Ter Braak 1988). Detrended correspondence analysis was used, detrending by segments as suggested by Knox (1989) and using non-linear rescaling (Økland 1986). CANOCO was then used to correlate the altitude and slope measures with each of the major axes obtained and to position the centroids of each of the main plant types on the ordination plot. These plant types were those noted as being dominant for each vegetation plot before it was harvested. This latter information will be used in Chapter 3 when looking at herbivore use in each habitat.

2.3 Results

Figure 2.1 shows the map produced from the aerial photos. The eight habitat types are outlined as are the major rivers and the 50m contour lines. It can be seen that the *Hagenia-Hypericum* woodland of the Saddle region dominated the study area and this

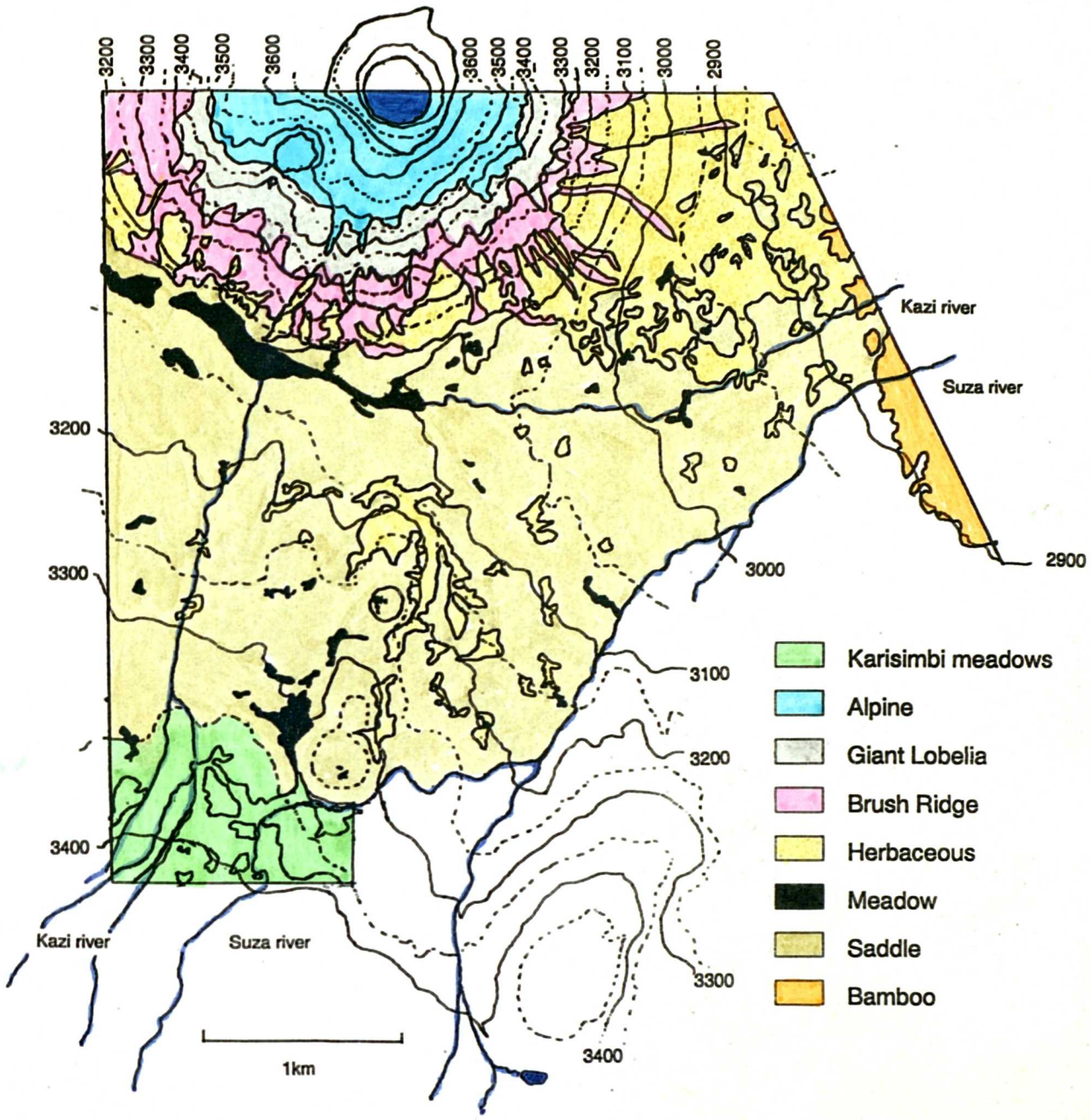
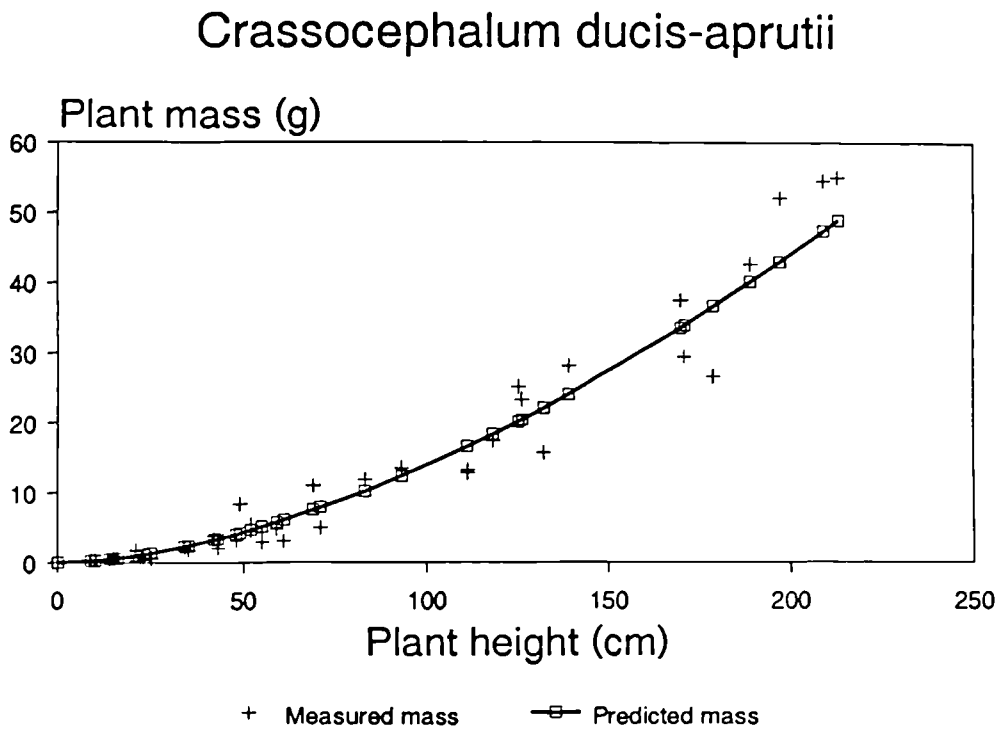


Figure 2.1 An orthographic projection of the study area taken from 1:20,000 scale aerial photos showing the position of the eight habitat types. Contour lines of 100 and 50 metres are marked as are the major rivers. The scale of the map varies with altitude, the scale marked being calculated at 3,100 metres (the altitude at which Karisoke lies).

Table 2.1. Areas of each of the eight habitat types in hectares taken from an orthographic projection of aerial photos of the study area. In calculating the areas both differences in scale due to increases in altitude and angle of slope have been taken into account.

	Area (ha)	Percentage of total
Bamboo	28.5	2.4%
Saddle	642.7	52.8%
Meadow	29.3	2.4%
Herbaceous	217.4	17.9%
Brush Ridge	96.4	7.9%
Giant *Lobelia*	64.7	5.3%
Alpine	68.5	5.6%
Karisimbi meadows	69.6	5.7%
Total	1217.1	100.0%



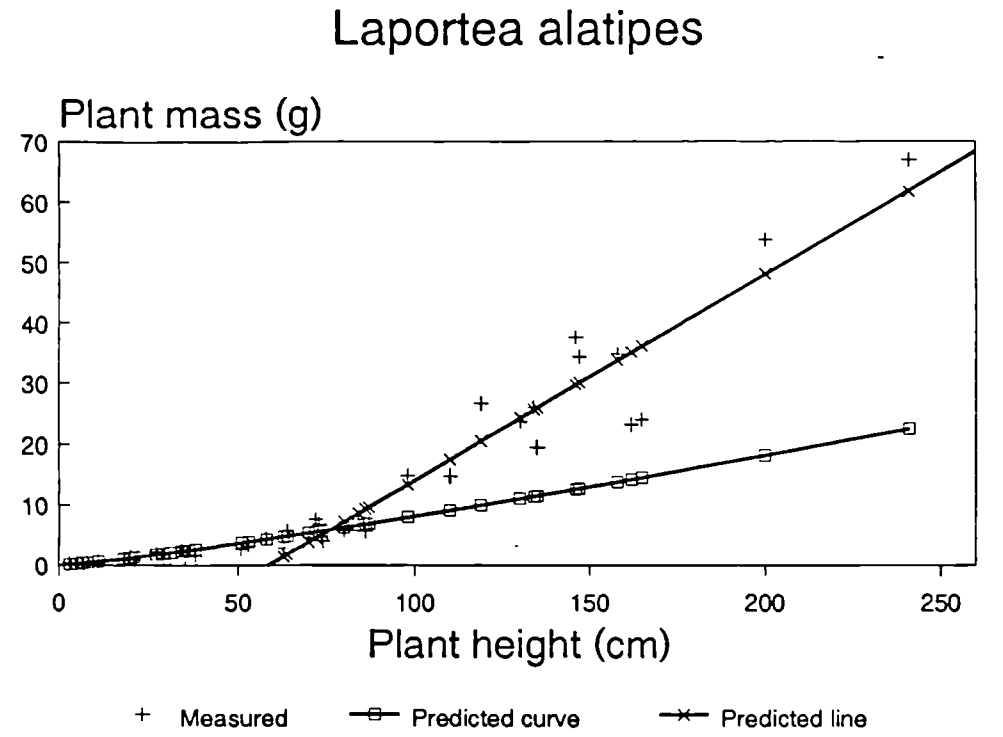


Figure 2.2 Plant height-mass relationships showing the two different models used. The top graph is a power curve of the form mass=a(height)^b. The second employs this form of curve at low hights but adds a linear response at higher heights. This latter form was necessary because fitting a curve of the above form through all the points overestimated the mass of the taller plants.

is confirmed from the relative areas of each habitat measured from the map (Table 2.1). Bamboo south of the Suza river was included in the study because it was too small a habitat to be worth studying separately north of the river and yet it was important that it was studied because it dominates other areas of the park. The total area of the study area was calculated as 12.17 km^2 (Table 2.1).

In order to assess the biomass of the tall herb species accurately, various equations were tried on the data to relate plant height or length to mass. For some species a simple curve of the form: mass = $a(height)^b$ could be fitted to the data. However for other plant species the initial stage of growth appeared to be curvilinear, after which there was a linear response. In these cases both a curve of the above form and a line were fitted separately, because the curve on its own overestimated the mass of the tall plants. Correlation coefficients for the curves were calculated using least squares regression on natural logarithms of mass and height. The values obtained for 'a' and 'b' from this regression were then corrected for the bias inherent in log-transformed data (Baskerville 1972, Sprugel 1983). Figure 2.2 shows two examples for the plant species *Crassocephalum ducis-aprutii* and *Laportea alatipes*, showing the simple curve and the curve and line fit respectively. Rice and Bazzaz (1989) found a similar response in *Abutilon theophrasti*. They plotted the natural logarithm of both height and mass to produce straight lines for some conditions of light intensity and to produce curves that appear to be linear initially which would fit the curve-line model I have used. There is some scatter of the data but this was to be expected as the samples were collected from several sites and will have experienced differences in light intensity and soil conditions. All of the regressions were highly significant (see Appendix 2).

At least 100 plots were sampled for plant biomass within each habitat type, although for the Saddle region more were sampled due to its large area. A total of 977 plots were sampled throughout the study area covering most of the region mapped in Figure

Table 2.2 Biomass (grams dry mass) of every plant species measured per square metre for each habitat type. Tall herbs have separate masses given for the total plant mass and the leaf mass.

SPECIES		BAMBOO	SADDLE	MEADOW	HERBACEOUS
Woody plants:					
Lobelia giberroa lvs.		2.35	13.49	19.74	
Rubus spp.			0.05		0.45
Hypericum revolutum lvs.		0.09	0.01		
Tall herbs:					
Crassocephalum	Total	9.21	63.63		179.17
ducis-aprutii	Leaf	2.93	16.12		39.77
Laportea alatipes	Total	14.96	57.59		60.19
	Leaf	4.83	16.43		15.38
Urtica massaica	Total	0.10	3.74		8.55
	Leaf	0.05	1.47		3.28
Senecio	Total	0.14	0.24		0.15
transmarinus	Leaf	0.04	0.07		0.04
Peucedanum linderi	Total	1.47	1.30		24.37
	Leaf	0.89	0.21		8.67
Peucedanum kerstenii			5.28		
Carduus nyassanus	Total	0.04	19.61	0.02	14.07
	Leaf	0.04	13.43	0.02	9.78
Echinops hoelenii	Leaf	0.05			1.14
Stachys aculeolata	Total	0.07	0.41		0.91
	Leaf	0.03	0.17		0.33
Senecio	Leaf		0.47		0.26
trichopterygius					
Oenanthe procumbens	Leaf	0.03	0.04		1.15
Solenostemon	Total	25.34	28.82		63.90
sylvaticum	Leaf	9.66	11.38		23.46
Plectranthus spp.	Total		12.65		17.73
	Leaf		4.56		6.40
Impatiens spp.	Total	4.51	9.45		13.81
	Leaf	1.53	3.89		4.58
Vines:					
Droquetia iners	Leaf	0.03	0.06		0.29
Galium spp.		0.39	1.41	0.28	4.18
Tylophoropsis sp.		0.10	0.01		0.02
Stephania abyssinica		0.17		0.92	
Gynura ruwenzoriensis	0.14			0.30	
Zehneria scabra			0.01		0.02

Table 2.2 continued.

Grasses:				
Carex bequaertii	0.14	0.81	36.35	1.25
Cyperus marii		1.38		
Carex simensis	0.77	3.77	0.35	0.56
Carex erythrorhiza		5.04	48.01	
Carex johnstonii		0.87		
Agrostis spp.	0.07	1.15	4.49	0.02
Poa annua		0.10		
Deschampsia flexuosa		0.17		
Festuca schimperiana	0.04	4.72		
Festuca engleri		1.41		0.36
Panicum striatissimum		6.26		
Luzula abyssinica		0.01	2.66	
Luzula johnstonii				
Mariscus Karisimbiensis	0.29	2.00		
Isolepis spp.			6.72	
Juncus dregeanus			0.25	
Small herbs:				
Senecio sabinjoensis				
Helichryssum globosum	0.03	16.31		
Hydroctyle spp.	0.41	3.20	1.30	0.58
Parochetus communis	0.10	0.57	0.10	0.03
Oxalis procumbens		0.01	0.07	
Trifolium spp.			0.22	
Stelleria sennii	0.05	0.67	0.02	0.10
Pilea rivularis	0.22	1.43		1.82
Alchemilla spp.		1.76	0.80	0.09
Alchemilla johnstonii		0.15		
Viola emminii	0.08	0.73	0.14	0.05
Mentha aquatica		0.14	0.37	
Ranunculus spp.	0.02	0.21	0.14	
Cerastium spp.		0.02	0.47	0.01
Hypericum peplidifolium	0.01	2.95		
Cardamine obliqua		0.01	0.23	0.06
Rumex bequaertii		0.03	0.06	
Rumex ruwenzoriense				0.01
Geranium arabicum		0.03	0.28	
Swertia macrosepala			1.48	
Polygonum nepalense	0.15			0.01
Plantago palmata		0.03		
Selaginella kraussiana	1.33	5.49	0.74	1.70
Total mass	62.27	242.48	143.40	417.97
Total leaf mass	26.43	112.77	143.40	146.81

Table 2.2 (continued).

SPECIES		BRUSH RIDGE	GIANT *LOBELIA*	ALPINE	KARISIMBI MEADOWS
Woody plants:					
Lobelia giberroa lvs.		14.55			
Rubus spp.		0.13	0.11	0.34	0.04
Hypericum revolutum lvs.		0.11	0.49	0.04	0.04
Tall herbs:					
Crassocephalum	Total	37.96	1.85	3.08	21.75
ducis-aprutii	Leaf	9.38	0.64	0.78	5.16
Laportea alatipes	Total	23.99	0.41		
	Leaf	7.05	0.12		
Urtica massaica	Total				
	Leaf				
Senecio	Total		0.83		
transmarinus	Leaf		0.23		
Peucedanum linderi	Total	0.94			
	Leaf	0.33			
Peucedanum kerstenii		0.02	2.76		
Carduus nyassanus	Total	25.40	16.58	0.44	7.24
	Leaf	19.87	13.69	0.20	4.32
Echinops hoelenii	Leaf				
Stachys aculeolata	Total	0.16	0.17	0.02	0.30
	Leaf	0.07	0.08	0.01	0.15
Senecio	Leaf	0.05			
trichopterygius					
Oenanthe procumbens	Leaf				
Solenostemon	Total	12.44			
sylvaticum	Leaf	4.70			
Plectranthus spp.	Total	13.08			
	Leaf	4.72			
Impatiens spp.	Total	1.46	0.38		
	Leaf	0.57	0.14		
Vines:					
Droquetia iners	Leaf	0.05			
Galium spp.		2.07	1.47	0.62	1.93
Tylophoropsis sp.		0.04			
Stephania abyssinica		0.04			
Gynura ruwenzoriensis					
Zehneria scabra					

Table 2.2 (continued).

Grasses:				
Carex bequaertii				0.42
Cyperus marii				
Carex simensis	1.79	3.20	7.76	15.32
Carex erythrorhiza		0.01	0.72	29.82
Carex johnstonii	8.89	2.79	1.88	
Agrostis spp.	0.40	1.37	4.38	4.38
Poa annua	0.24	0.01	0.18	0.03
Deschampsia flexuosa				
Festuca schimperiana	0.03	1.05	6.48	5.45
Festuca engleri	2.70	34.27	0.38	7.39
Panicum striatissimum			1.50	
Luzula abyssinica	0.01	0.71	1.93	3.13
Luzula johnstonii		0.15	1.77	0.99
Mariscus Karisimbiensis				
Isolepis spp.			1.10	0.39
Juncus dregeanus				
Small herbs:				
Senecio sabinjoensis		0.29	0.03	
Helichrysum globosum				
Hydroctyle spp.	3.33	4.40	1.19	6.83
Parochetus communis	0.2	0.469		0.40
Oxalis procumbens				0.05
Trifolium spp.				
Stelleria sennii	0.51	1.21	0.01	0.81
Pilea rivularis	0.83	2.23	0.03	1.09
Alchemilla spp.	0.34	1.52	0.37	2.08
Alchemilla johnstonii	0.80	7.97	18.22	
Viola emminii	0.46	0.47	0.25	1.05
Mentha aquatica	0.05	0.66		0.02
Ranunculus spp.	0.03			0.08
Cerastium spp.		0.10	0.02	0.18
Hypericum peplidifolium			1.32	
Cardamine obliqua	0.02		0.18	
Rumex bequaertii				
Rumex ruwenzoriense		0.82		
Geranium arabicum				0.07
Swertia macrosepala		0.11	1.97	0.19
Polygonum nepalense		0.15		
Plantago palmata				
Selaginella kraussiana	6.53	1.79		2.71
Total mass	158.89	80.55	46.12	135.07
Total leaf mass	90.17	75.24	43.57	115.41

Table 2.3 Percentages of the total herb biomass that different plant types formed in each of the eight habitat types. The data is given for total plant mass and also plant leaf mass which excludes the stem mass of the tall herbs.

TOTAL PLANT MASS

	Woody leaves	Tall herbs	Vines	Grasses	Small herbs
Bamboo	3.8	89.8	1.0	1.6	3.8
Saddle	5.6	81.6	0.8	6.1	5.9
Meadow	0.1	3.6	0.2	78.1	18.0
Herbaceous	4.8	92.2	1.4	0.5	1.1
Brush Ridge	9.3	72.7	1.4	8.9	7.7
Giant *Lobelia*	0.7	25.1	1.8	54.0	18.3
Alpine	0.8	13.7	1.3	57.6	26.6
Karisimbi meadows	0.1	21.6	1.4	50.9	26.0

PLANT LEAF MASS

	Woody leaves	Tall herbs	Vines	Grasses	Small herbs
Bamboo	8.9	76.0	2.5	3.7	8.9
Saddle	12.1	60.5	1.5	13.2	12.7
Meadow	0.1	3.6	0.2	78.1	18.0
Herbaceous	13.8	77.8	3.9	1.5	3.0
Brush Ridge	16.4	51.9	2.4	15.6	13.7
Giant *Lobelia*	0.8	19.8	2.0	57.8	19.6
Alpine	0.9	8.6	1.4	60.9	28.2
Karisimbi meadows	0.1	8.3	1.7	59.5	30.4

2.1. The mean biomass per square metre for each plant species is given in Table 2.2 for each habitat type and Table 2.3 summarises this data in terms of vegetation types. Appendix 3 gives the total mass and standard error of each plant species within the study area (multiplying the results in Table 2.2 by the area of each vegetation type in table 2.1).

The results of the DCA ordination on the Saddle vegetation showed that this habitat could be separated floristically into geographical divisions, east and west of the hills south of Karisoke or northern and southern halves of the study area. The biomasses of these regions are similarly given in Table 2.4. The mean altitude for each habitat was calculated and in the case of the Saddle region it was calculated for the western and eastern sectors. If this is plotted against total plant biomass it can be seen that apart from the Bamboo zone, total biomass decreases with altitude as does species richness (Figure 2.3). It must be remembered, however, that these are only herbaceous plants that are being measured. The biomass of trees and bamboo stems would alter the picture, as would the biomass of inaccessible foliage. Species richness will also be altered by the inclusion of mosses, ferns, epiphytic plants and vines in the canopy of the bamboo: these were not included as they were not obviously eaten by the herbivore species.

Both Simpson and Shannon-Wiener diversity indices were calculated from these biomass values and these are given in Table 2.5. It can be seen that diversity increased slightly with altitude (Figure 2.4). This is because species evenness or equitability (Peet 1974) was greater at higher altitudes, which meant that at the lower altitudes there were a few species that dominated the total plant biomass. If the same data are plotted for only leaf biomass (Figures 2.5 and 2.6 and Table 2.5) it can be seen that, whilst leaf mass decreased with altitude, diversity hardly changed. This is because it was the tall-stemmed herbs which were dominating at the lower altitudes.

Table 2.4 The biomass (grams) of each plant species in different areas of the Saddle habitat type. The habitat is divided into north or south and east or west.

SPECIES		NORTH	SOUTH	WEST	EAST
Woody plants:					
Lobelia giberroa lvs.		13.78	13.26	12.46	14.33
Rubus spp.		0.05	0.04	0.10	
Hypericum revolutum lvs.		0.15	0.04	0.13	0.05
Tall herbs:					
Crassocephalum	Total	28.50	92.53	31.19	89.93
ducis-aprutii	Leaf	7.03	23.59	8.87	21.99
Laportea alatipes	Total	58.95	56.46	32.57	77.86
	Leaf	18.20	14.97	10.51	21.22
Urtica massaica	Total	5.32	2.44	6.49	1.51
	Leaf	2.14	0.92	2.63	0.53
Senecio	Total		0.44	0.54	
transmarinus	Leaf		0.13	0.16	
Peucedanum linderi	Total	1.52	1.11	1.14	1.42
	Leaf	0.11	0.30	0.35	0.11
Peucedanum kerstenii					
Carduus nyassanus	Total	25.82	14.49	21.34	18.20
	Leaf	18.12	9.56	12.62	14.08
Echinops hoelenii	Leaf				
Stachys aculeolata	Total	0.27	0.53	0.43	0.39
	Leaf	0.12	0.22	0.19	0.16
Senecio	Leaf		0.85		0.85
trichopterygius					
Oenanthe procumbens	Leaf	0.07	0.01		0.06
Solenostemon	Total	15.51	39.77	3.02	49.74
sylvaticum	Leaf	6.21	15.63	1.31	19.54
Plectranthus spp.	Total	3.76	19.96	26.43	1.49
	Leaf	1.60	6.98	9.35	0.67
Impatiens spp.	Total	7.15	11.35	17.04	3.30
	Leaf	2.73	4.83	7.24	1.17
Vines:					
Droquetia iners	Leaf	0.06	0.05		0.10
Galium spp.		0.82	1.90	0.77	1.94
Tylophoropsis sp.			0.01		0.01
Stephania abyssinica		0.03	0.28		0.30
Gynura ruwenzoriensis					
Zehneria scabra			0.03		0.03

Table 2.4 (continued)

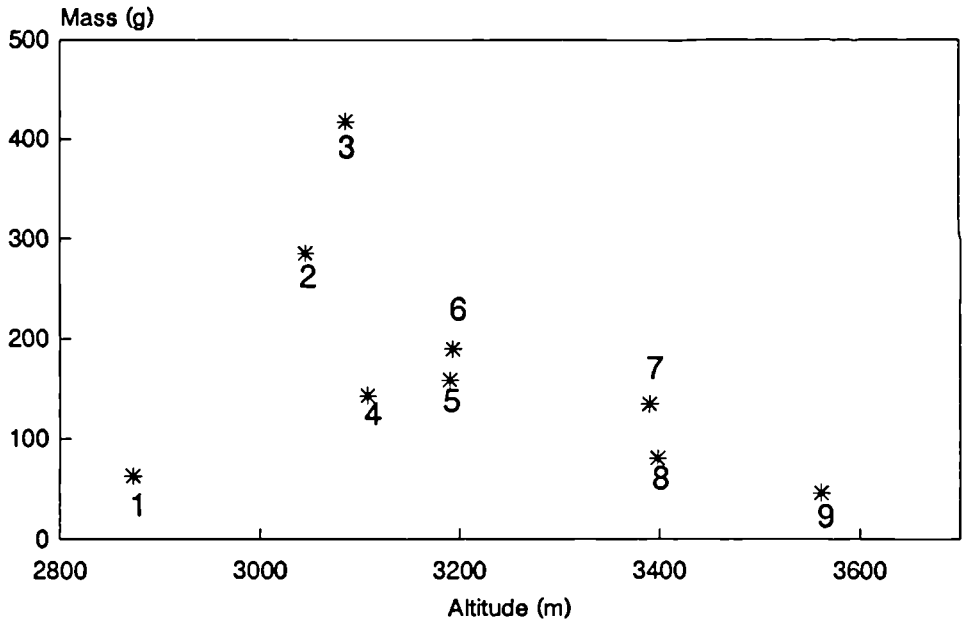
Grasses:				
Carex bequaertii	0.72	0.88		1.46
Cyperus marii	2.33	0.60		2.50
Carex simensis	4.06	3.54	5.96	2.01
Carex erythrorhiza	10.20	0.80	6.45	3.90
Carex johnstonii	0.34	1.30	0.43	1.23
Agrostis spp.	2.20	0.28	1.78	0.64
Poa annua	0.19	0.03	0.19	0.03
Deschampsia flexuosa				
Festuca schimperiana	0.07	0.08		
Festuca engleri	1.78	1.10	2.50	0.52
Panicum striatissimum				
Luzula abyssinica	0.03			0.03
Luzula johnstonii				
Mariscus Karisimbiensis	0.18	0.38		0.52
Isolepis spp.				
Juncus dregeanus				
Small herbs:				
Senecio sabinjoensis				
Helichryssum globosum	0.06		0.06	
Hydroctyle spp.	4.65	2.00	4.28	2.32
Parochetus communis	0.86	0.34	0.88	0.33
Oxalis procumbens	0.01		0.01	
Trifolium spp.				
Stelleria sennii	0.77	0.59	1.13	0.30
Pilea rivularis	1.66	1.24	0.20	2.43
Alchemilla spp.	2.66	1.01	2.76	0.94
Alchemilla johnstonii				
Viola emminii	0.94	0.55	0.86	0.62
Mentha aquatica	0.30		0.08	0.18
Ranunculus spp.	0.30	0.14	0.34	0.11
Cerastium spp.	0.05		0.04	0.01
Hypericum peplidifolium	0.01	0.02		0.03
Cardamine obliqua	0.02		0.02	
Rumex bequaertii	0.04	0.02	0.04	0.02
Rumex ruwenzoriense				
Geranium arabicum	0.07		0.03	0.03
Swertia macrosepala		0.11		
Polygonum nepalense	0.28	0.04	0.31	0.02
Plantago palmata	0.07		0.04	0.03
Selaginella kraussiana	8.20	3.26	7.82	3.60
Total mass	204.74	273.85	189.94	285.32
Total leaf mass	114.10	111.90	102.98	120.95

Figure 2.3 Total plant mass and species richness for each of the habitat types (using the data for the eastern and western sections of the Saddle) plotted against the mean altitude of the sample of plots. Apart from the Bamboo zone at the lowest altitude there was a decrease with both mass and species richness with altitude.

Key:

1= Bamboo
2= Herbaceous
3= Saddle (east)
4= Meadow
5= Saddle (west)
6= Brush Ridge
7= Karisimbi meadows
8= Giant *Lobelia*
9= Alpine

Mass per square metre
Total mass



Species Richness

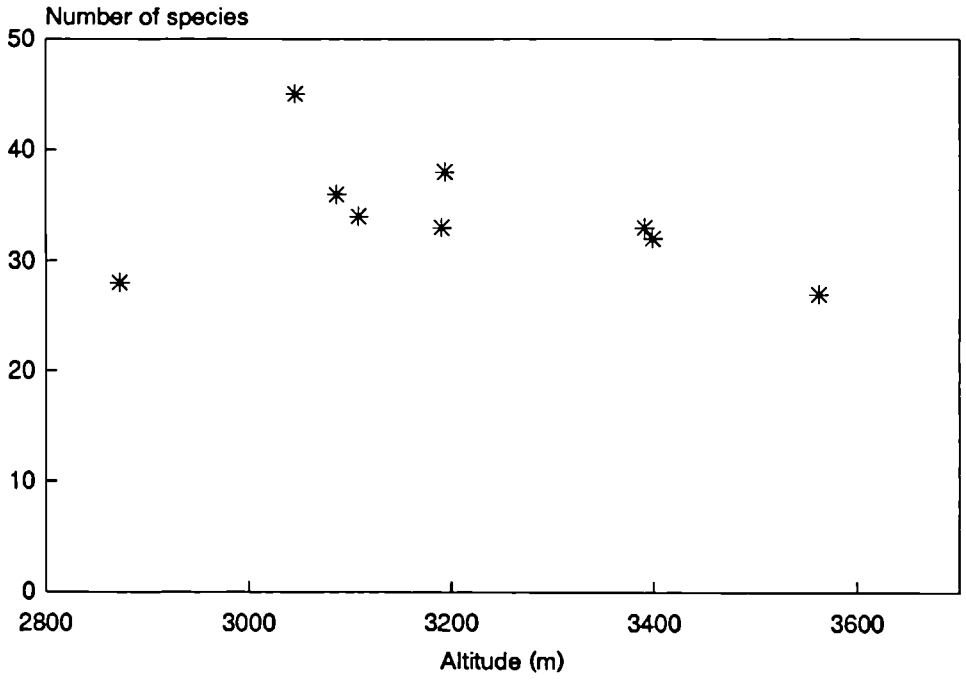
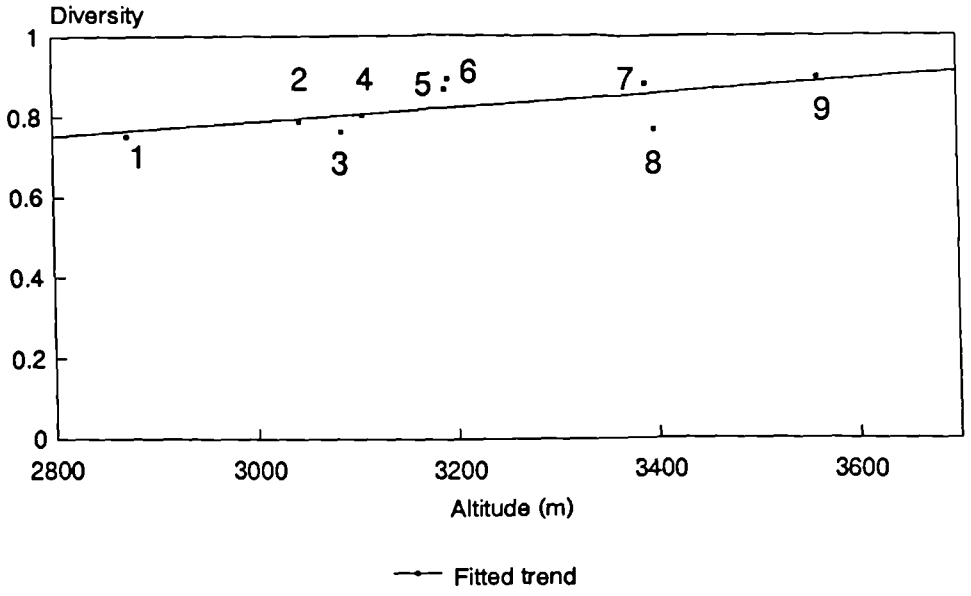


Figure 2.4 Diversity and equitability of the total plant mass plotted against mean altitude for each habitat type (the Saddle zone being divided into eastern and western regions).

Key:

1= Bamboo
2= Herbaceous
3= Saddle (east)
4= Meadow
5= Saddle (west)
6= Brush Ridge
7= Karisimbi meadows
8= Giant *Lobelia*
9= Alpine

Simpson's Diversity Index
Total plant mass



Equitability
Total mass

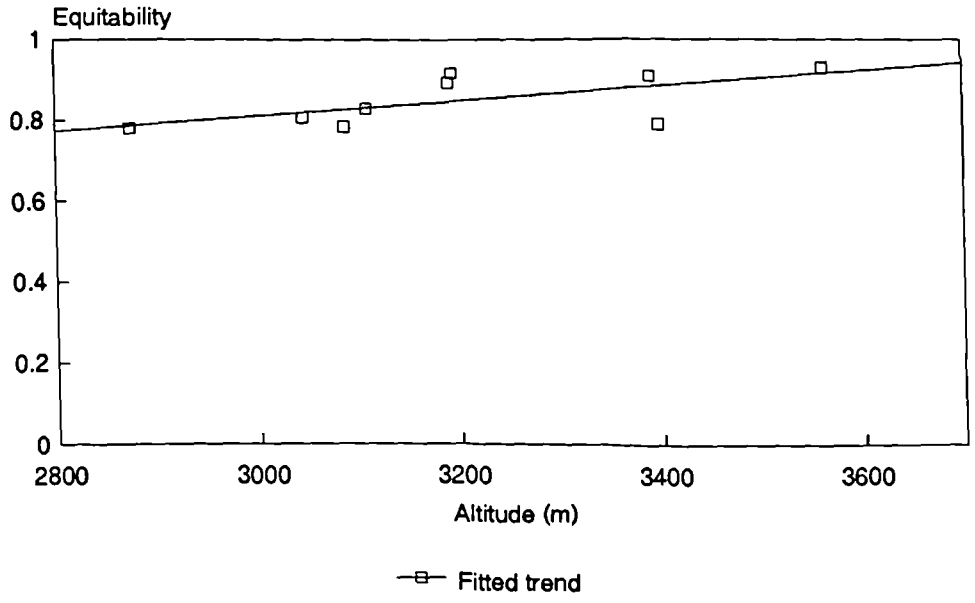


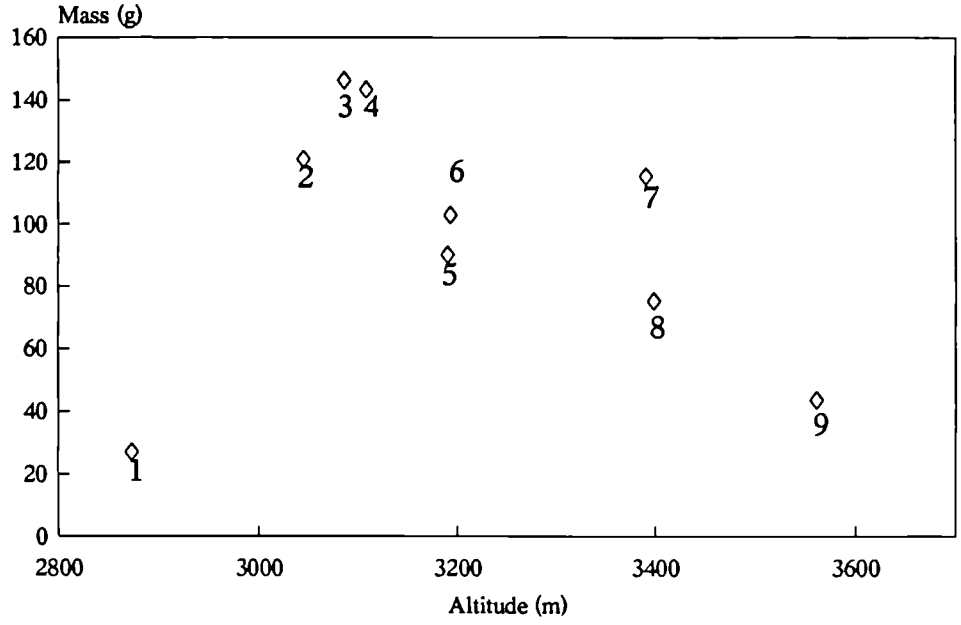
Figure 2.5 Total leaf mass and species richness plotted against altitude showing a similar downward trend as altitude increases (see Figure 2.4).

Key:

1= Bamboo
2= Herbaceous
3= Saddle (east)
4= Meadow
5= Saddle (west)
6= Brush Ridge
7= Karisimbi meadows
8= Giant *Lobelia*
9= Alpine

Mass per square metre

Leaf mass



Species Richness

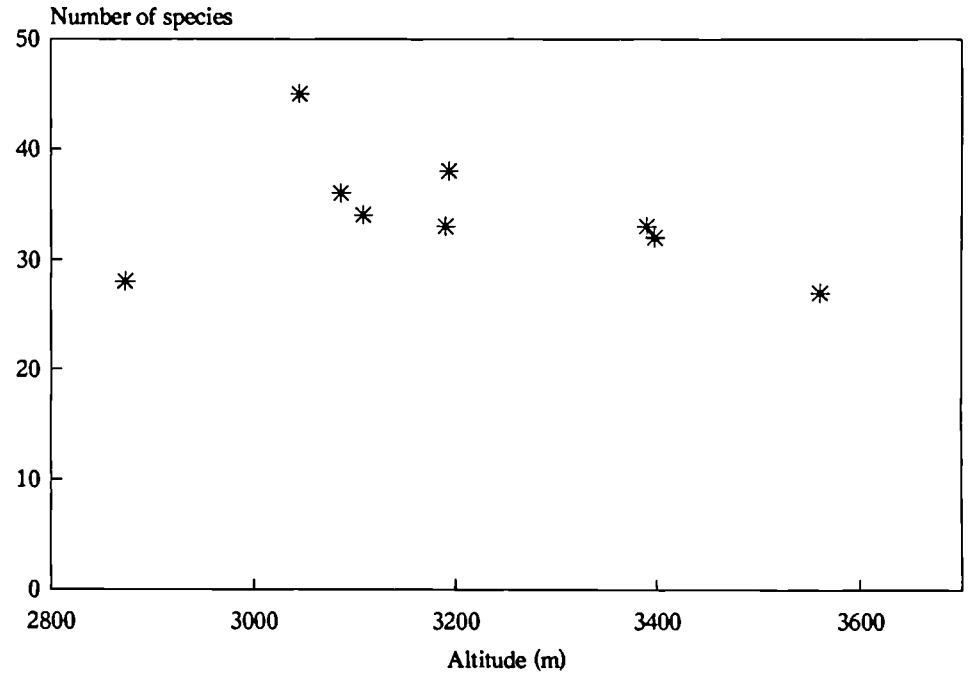
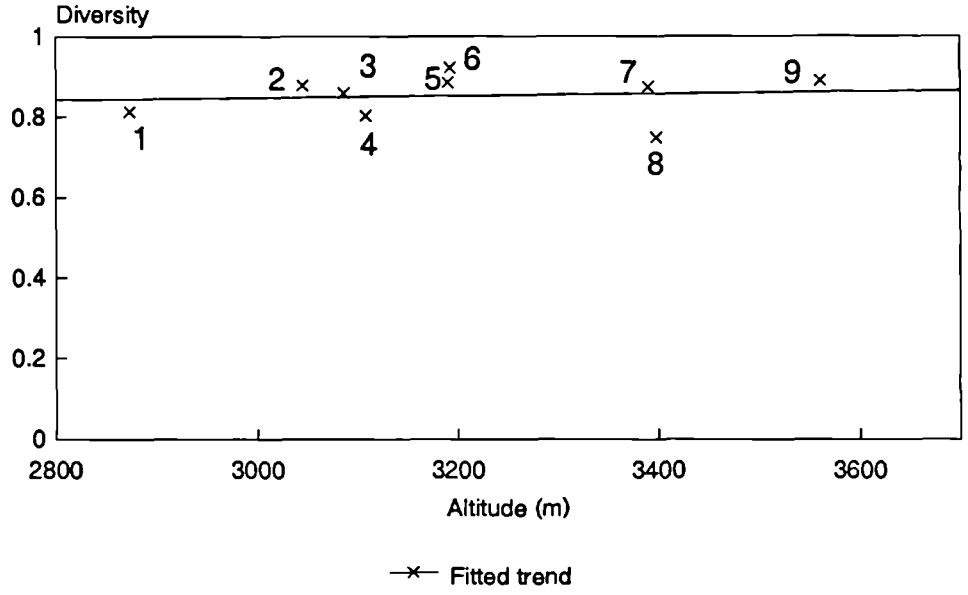


Figure 2.6 Diversity and equitability of the leaf biomass data plotted against mean altitude. Unlike the same data for the total mass (Figure 2.5) there did not seem to be an increase in either diversity or equitability with altitude.

Key:

1= Bamboo
2= Herbaceous
3= Saddle (east)
4= Meadow
5= Saddle (west)
6= Brush Ridge
7= Karisimbi meadows
8= Giant *Lobelia*
9= Alpine

Simpson's Diversity Index
Leaf mass



Equitability
Leaf mass

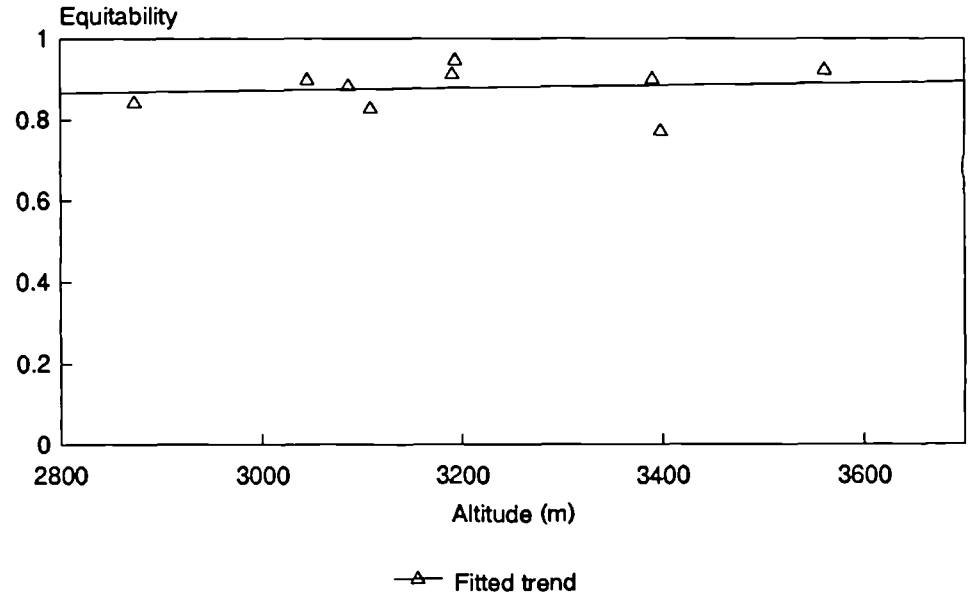


Table 2.5 Diversity indices, equitability and species richness for each of the eight habitat types. Both Simpson's index and the Shannon-Wiener index of diversity are given.

	BAMBOO	SADDLE	MEADOW	HERB.	BRUSH RIDGE	GIANT *LOBELIA*	ALPINE	KARISIMBI MEADOWS
Simpson's: (1-D)								
Total mass	0.752	0.845	0.803	0.762	0.867	0.767	0.896	0.881
Leaf mass	0.813	0.909	0.803	0.859	0.885	0.749	0.889	0.874
Shannon-Wiener:								
Total mass	2.577	3.340	3.039	2.750	3.338	3.070	3.692	3.580
Leaf mass	3.076	3.944	3.039	3.369	3.552	2.973	3.622	3.592
Equitability:								
Total mass	0.780	0.863	0.828	0.784	0.894	0.792	0.931	0.909
Leaf mass	0.843	0.928	0.828	0.884	0.912	0.773	0.923	0.901
Richness:								
Species number	28	49	34	36	33	32	27	33

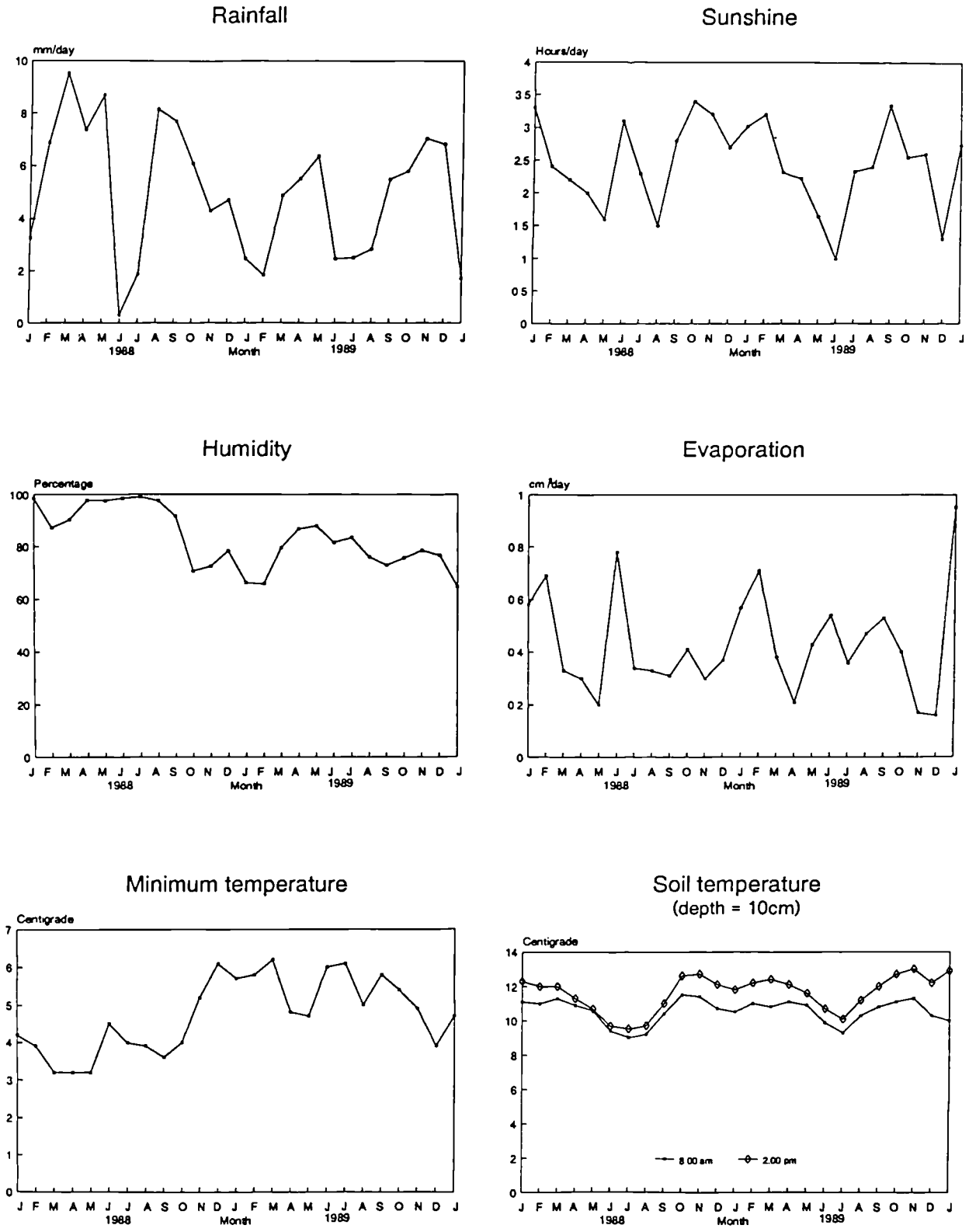
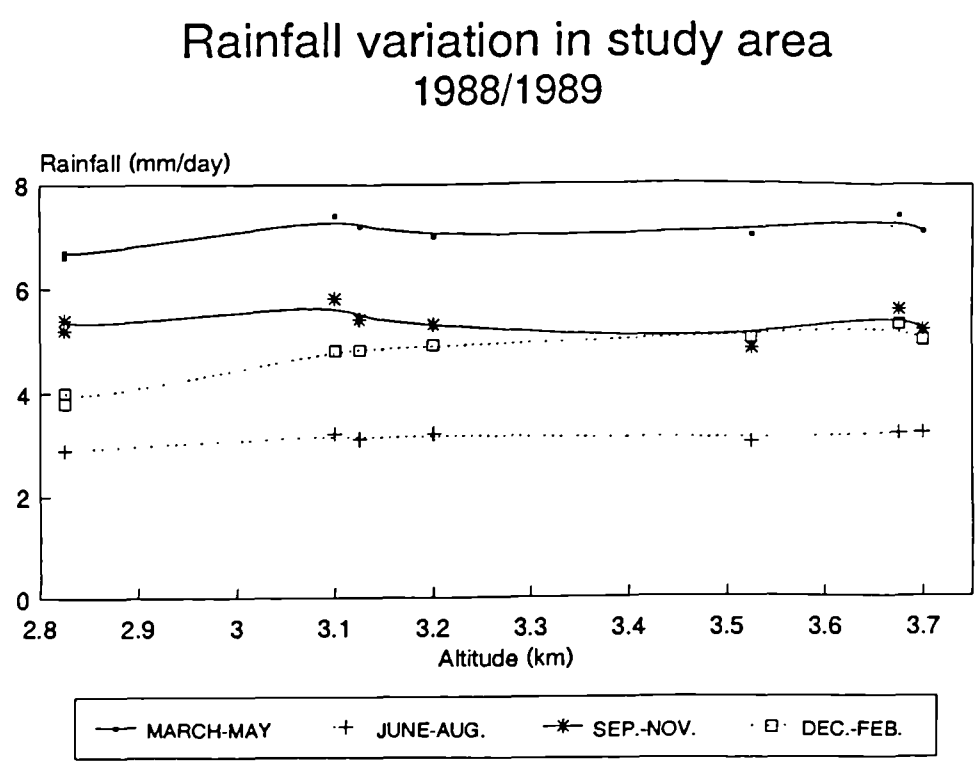


Figure 2.7 Climatological data collected at the Karisoke research centre over the two years of the study. 1988 was an exceptionally wet and cold year as far as past records go (Hastings & Byers in press).



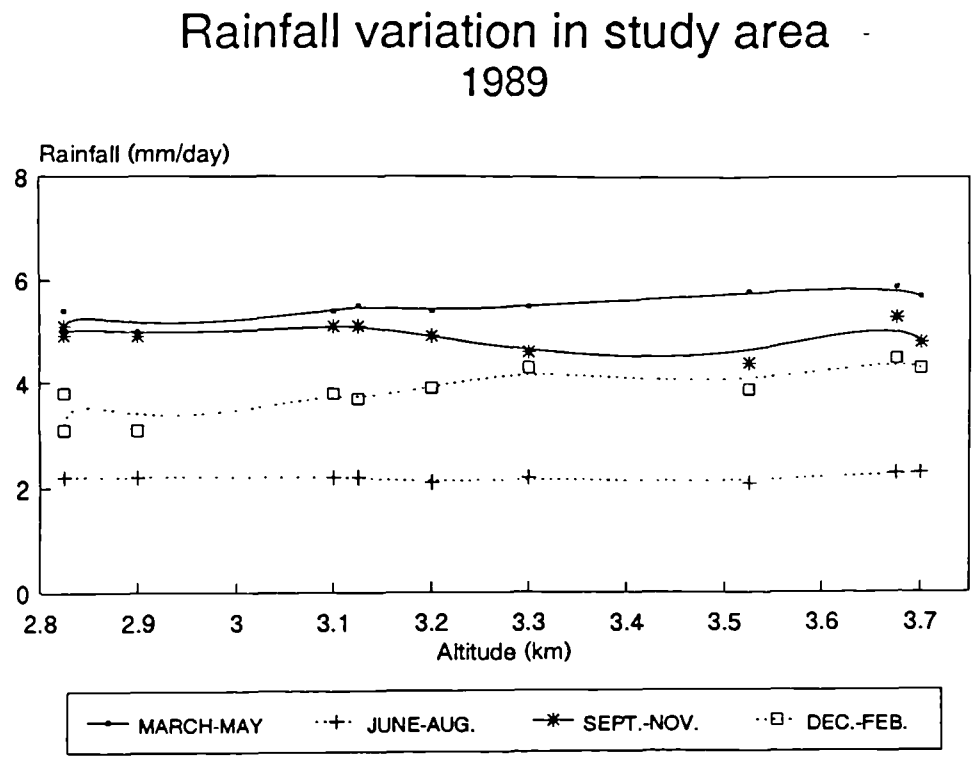


Figure 2.8 Rainfall data collected on Bisoke at weekly intervals plotted for each season against the altitude of the rain guage. The top graph shows data for two years from rain guages up the western side of Bisoke and down near the edge of the park by the Suza river. In 1989 two further guages were placed up the eastern side of Bisoke to see if there was any obvious difference but as can be seen from the lower graph this was not the case.

Climatological data for Karisoke over the two years are summarised in Figure 2.7. Rainfall is bimodal in pattern but, as can be seen from the graph, the amount of rainfall in each season can vary between years. The study of the herbivore habitat use and diet was done separately for the two wet seasons (March - May and September - November) and the two drier seasons (June - August and December - February). The biomass of the vegetation did not appear to vary greatly between seasons in 1988, so that only one measure of plant biomass was obtained between June and November 1989. It has been suggested that the highest rainfall in the park is to be found near the park boundary at the lower altitudes (Jost 1987). Rainfall gauges placed on Bisoke did not show this and in some seasons there was an increase in rainfall with altitude (Fig. 2.8). From these data all plants would appear to experience similar rainfall over a three-monthly period. This is also found if the data are examined for each month separately.

The results of the DCA ordinations are given in Figures 2.9 to 2.16. The first two DCA axes are plotted against each other with the axis scale measured in units of species turnover or standard deviations. The environmental variables and the plant type centroids are plotted on acetate so that they can be laid over the plant species plot and a subjective interpretation is given to the axes based on the species found at each end. The arrows representing the environmental variables, altitude and slope, are plotted at the same magnitude on each ordination plot which allows their relative lengths to be compared (the scale of the axes must be considered when calculating these lengths). Dropping a perpendicular line from a plant species to the arrow shows where it lies with respect to other plants on an increasing altitudinal gradient or gradient of slope. For example, in Figure 2.9 *Carex simensis* (C.Sim) is generally found at high altitudes in the Bamboo whilst *Urtica massaica* is found at low altitudes. The eigenvalues for each of the axes and the correlation coefficients between the axes and the environmental variables are given in Table 2.6. The eigenvalue is a measure of the separation of the distribution of the species along the

Figure 2.9 Ordination of plant leaf mass data in the Bamboo zone. Axis one separates the dense stands of bamboo stems where little else grows (on the right) from the more open herbaceous areas. Axis two seems to separate the the smalller herbs and grasses at the top of the plot from the denser aggregations of taller herbs at the bottom.

Key:

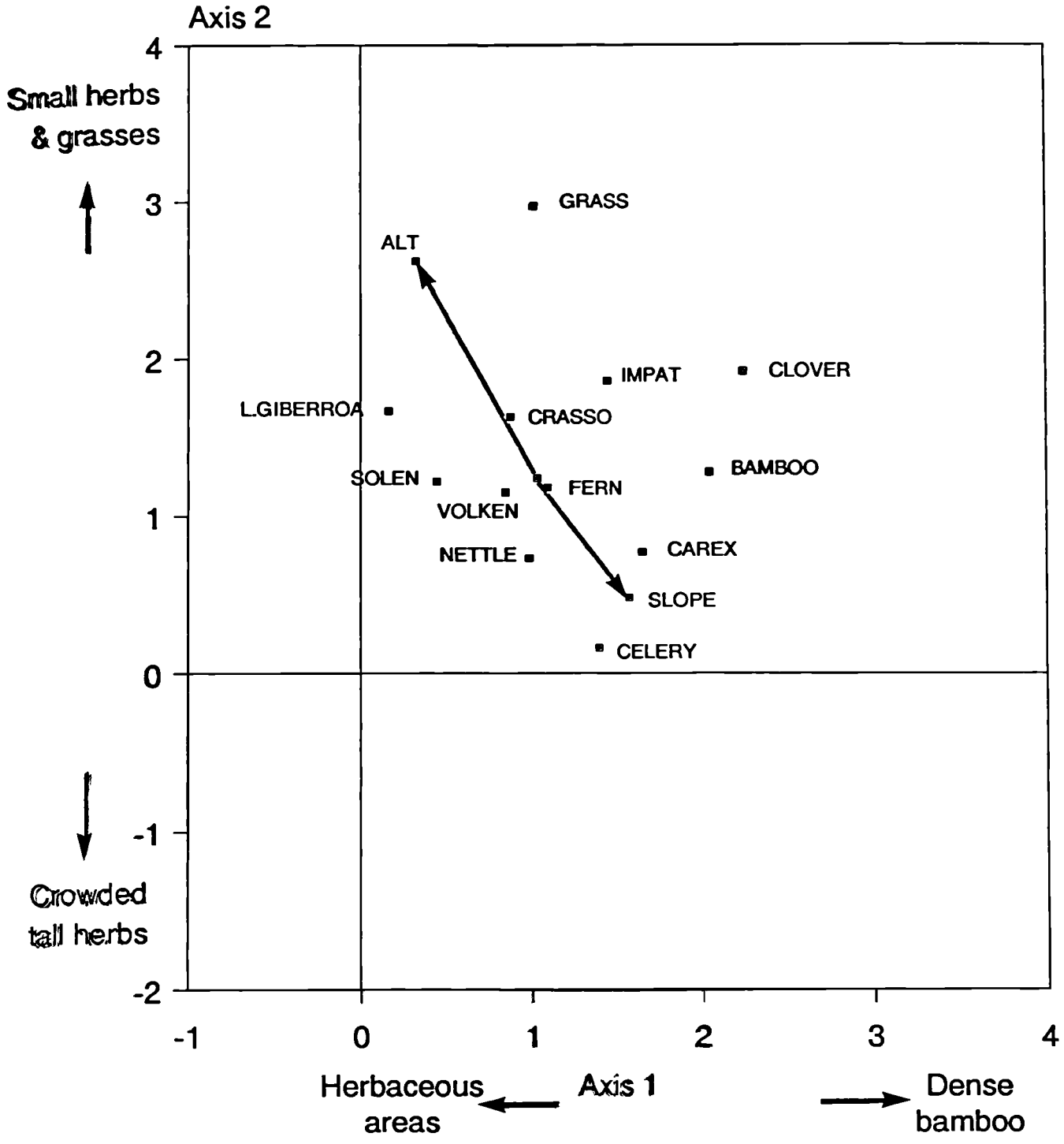
Plant species:

Agr = *Agrostis* spp., C.sim = *Carex simensis,* Arund = *Arundinaria alpina* (bamboo. st=stem lf=leaf). C.Beq = *Carex bequaertii*, Hyd = *Hydroctyle* spp., P.comm = *Parochetus communis*, Viol = *Viola emminii*, Stell = *Stellaria sennii*, Ran = *Ranunculus sps*, Gal = *Galium* spp., Sel = *Selaginella kraussiana*, Pilea = *Pilea rivularis*, Impat = *Impatiens sps*, Droq = *Droquetia iners*, Oenan = *Oenanthe procumbens*, C.Nya = *Carduus nyassanus,* Echin = *Echinops hoelenii*, S.Trich = *Senecio trichopterygius*, Crasso = *Crassocephalum ducis-aprutii*, Stach = *Stachys aculeolata*, S.Trans = *Senecio transmarinus*, Solen = *Solenostemon sylvaticum*, Lap = *Laportea alatipes*, Tylo = *Tylophoropsis heterophylla*, P.Lind = *Peucedanum linderi*, Gynura = *Gynura ruwenzoriensis*, Urtic = *Urtica massaica*, L.gibb = *Lobelia giberroa*

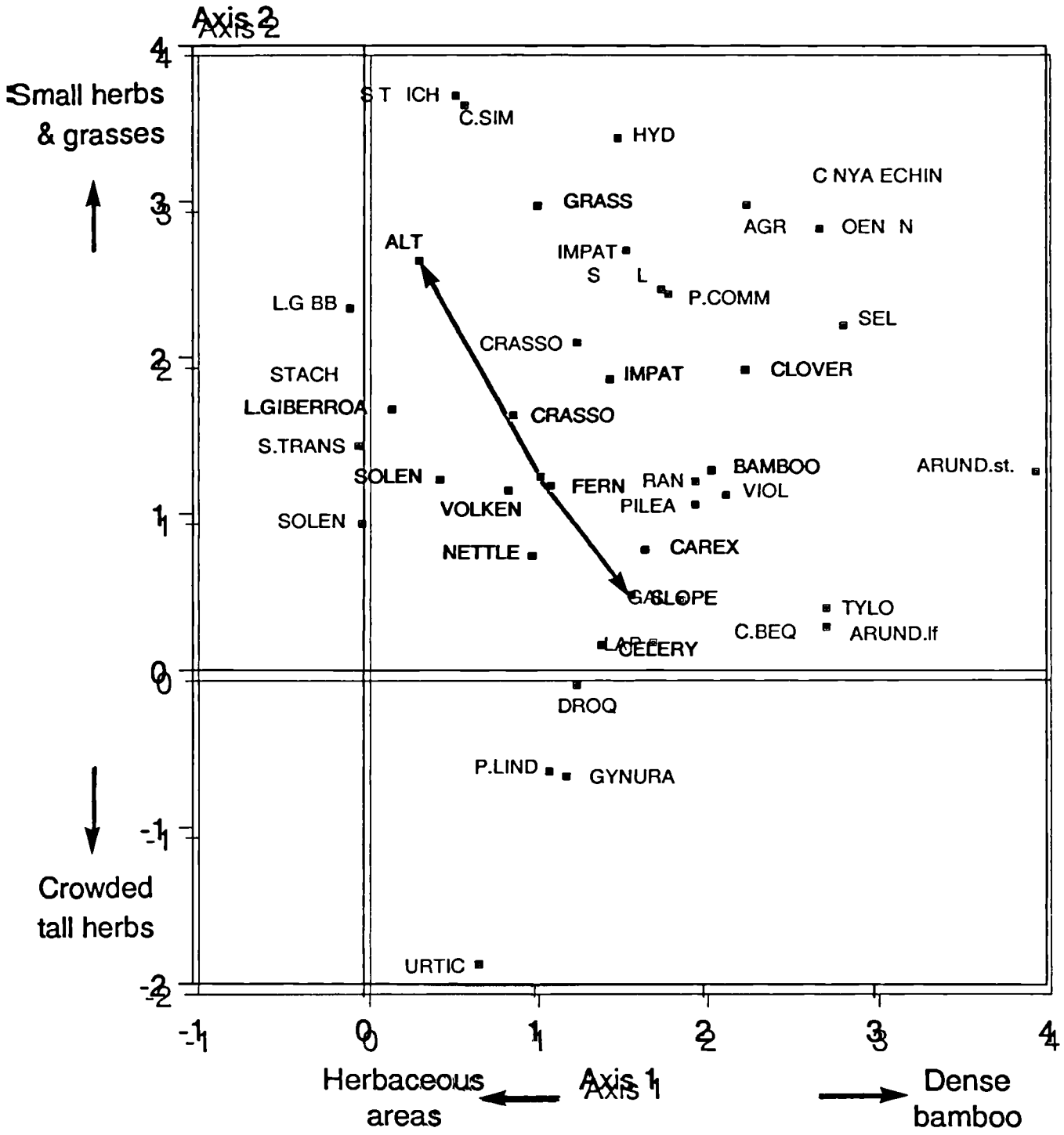
Vegetation types/Environmental variables:

Impat = *Impatiens* spp., Volken = *Volkensia ruwenzoriensis*, Crasso = *Crassocephalum ducis-aprutii*, Solen = *Solenostemon sylvaticum*, Alt = Altitude

Bamboo


Axis 2
4
3
2
1
0
-1
-2
Small herbs & grasses
Crowded tall herbs
GRASS
ALT
IMPAT
CLOVER
LGIBERROA
CRASSO
BAMBOO
SOLEN
FERN
VOLKEN
NETTLE
CAREX
SLOPE
CELERY
-1
0
1
2
3
4
Herbaceous areas
Axis 1
Dense bamboo

Bamboo


Axis 2
Small herbs & grasses
Crowded tall herbs
Herbaceous areas
Axis 1
Dense bamboo
S T ICH
C.SIM
HYD
C NYA ECHIN
GRASS
AGR
OEN N
ALT
IMPAT
S L
P.COMM
L.G BB
SEL
CRASSO
STACH
IMPAT
CLOVER
L.GIBERROA
CRASSO
S.TRANS
BAMBOO
ARUND.st.
SOLEN
FERN
RAN
VIOL
VOLKEN
PILEA
SOLEN
CAREX
NETTLE
SLOPE
TYLO
C.BEQ
ARUND.lf
CELERY
DROQ
P.LIND
GYNURA
URTIC

Bamboo

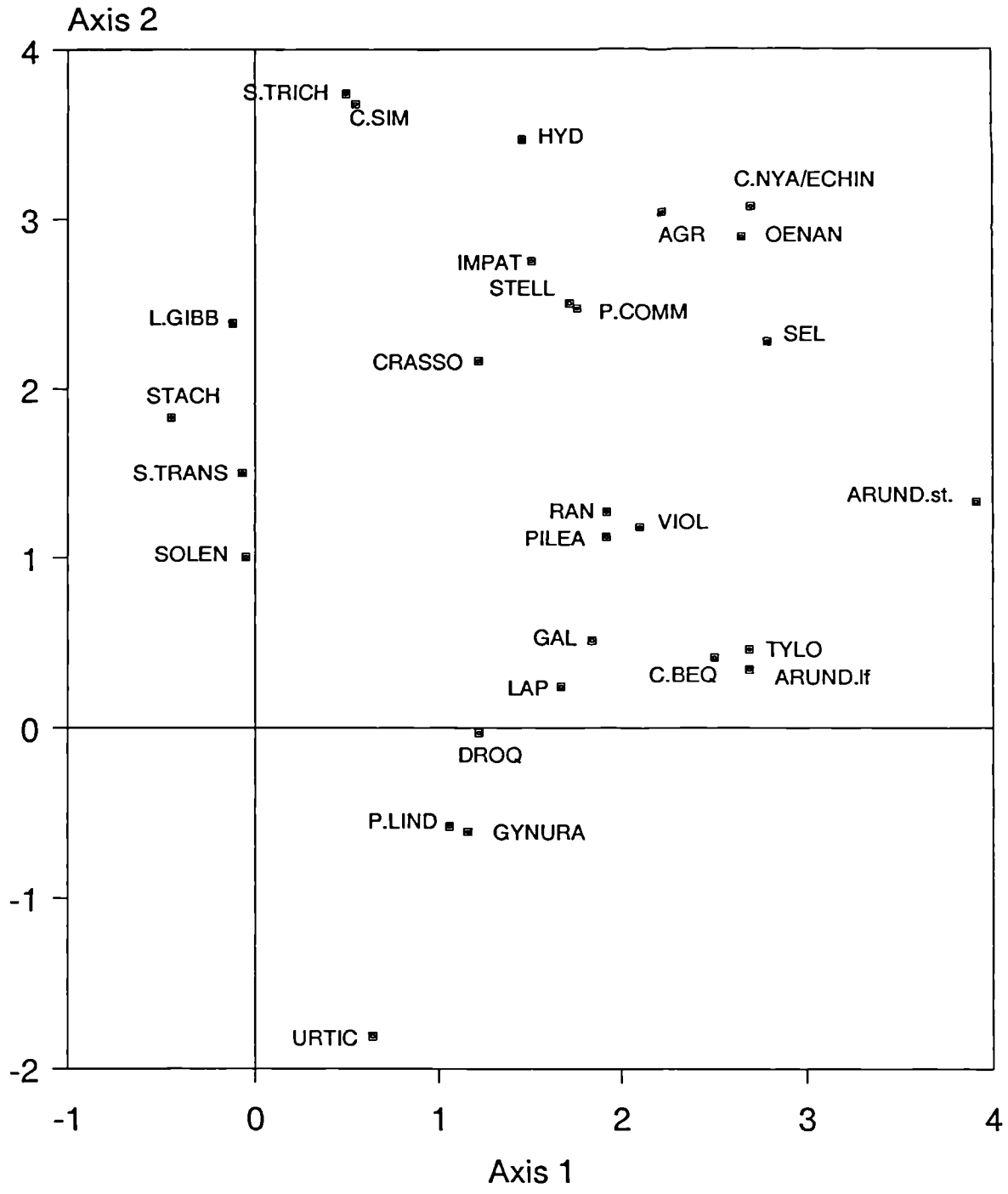

Axis 2
4
3
2
1
0
-1
-2
S.TRICH
C.SIM
HYD
C.NYA/ECHIN
AGR
OENAN
IMPAT
STELL
P.COMM
L.GIBB
SEL
CRASSO
STACH
S.TRANS
ARUND.st.
RAN
VIOL
PILEA
SOLEN
GAL
TYLO
C.BEQ
ARUND.lf
LAP
DROQ
P.LIND
GYNURA
URTIC
-1
0
1
2
3
4
Axis 1

Figure 2.10 Ordination of plant leaf mass in the Saddle zone. Axis one separates the grasses and small herbs on the left from the tall stemmed herbs on the right. This is similar to the north-south split seen in table 2.4. Axis two separates those plants found west of the hills south of Karisoke at the bottom of the plot from those in the east at the top of the plot. Plotting the ordination of the sample plots does seem to agree with this although there is a fair degree of overlap.

Key:

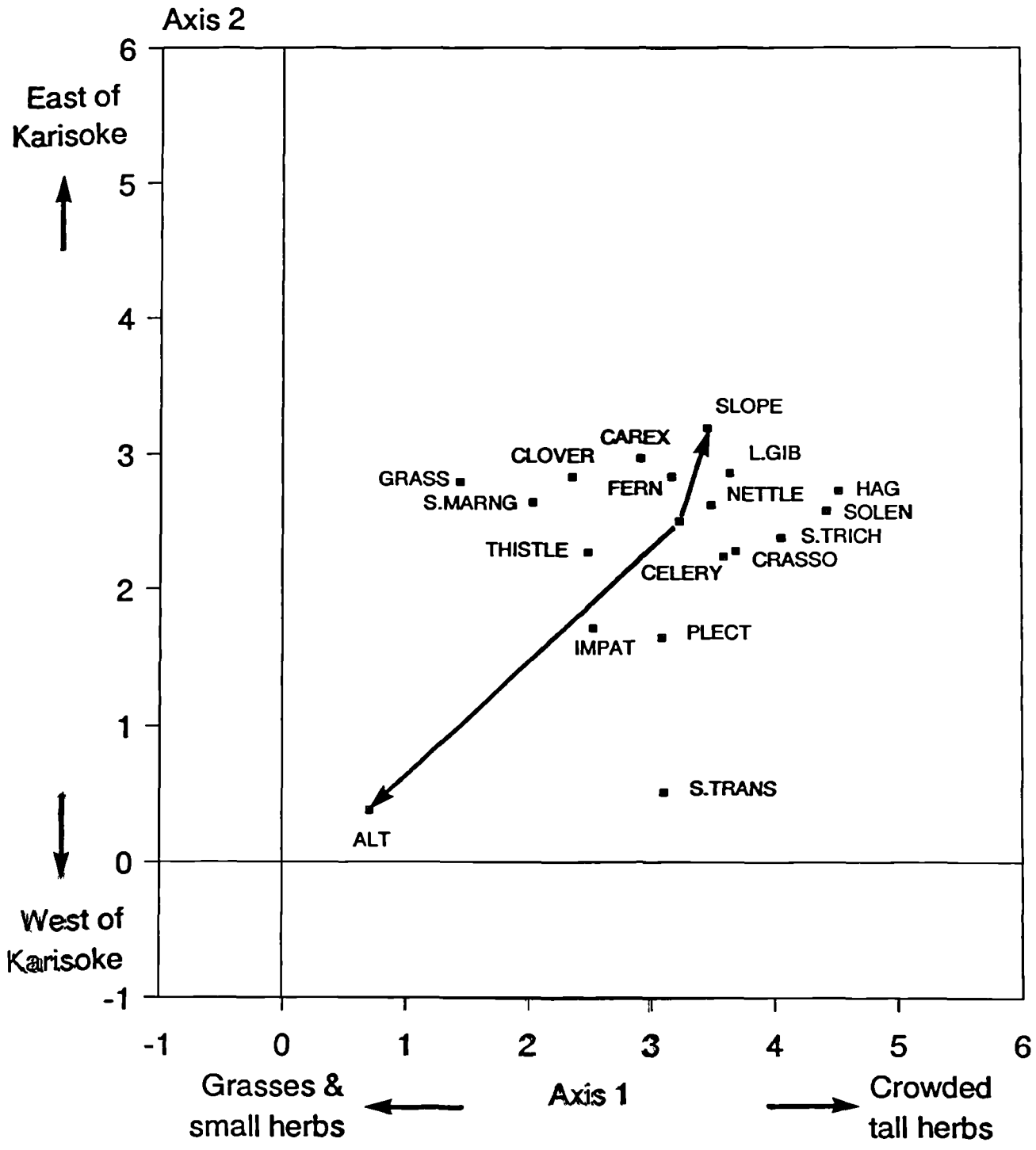
Plant species:

Agr = *Agrostis* spp., C.ery = *Carex erythrorhiza*, C.sim = *Carex simensis*, C.joh = *Carex johnstonii*, Cyp = *Cyperus dichroostachyus*, C.Beq = *Carex bequaertii*, Luz.A = *Luzula abyssinica*, P.ann = *Poa annua*, F.engl = *Festuca engleri*, F.sch = *Festuca schimperiana*, Marisc = *Mariscus karisimbiensis*, Ceras = *Cerastium* spp., Card = *Cardamine obliqua*, Hyd = *Hydroctyle* spp., P.comm = *Parochetus communis*, Oxa = *Oxalis procumbens*, Viol = *Viola emminii*, Ment = *Mentha aquatica*, Ger = *Geranium arabicum*, Alch = *Alchemilla* spp., Poly = *Polygonum nepalense*, Plan = *Plantago palmata*, Rum.b = *Rumex bequaertii*, Stell = *Stellaria sennii*, Ran = *Ranunculus* spp., Gal = *Galium* spp., Sel = *Selaginella kraussiana*, Pilea = *Pilea rivularis*, Impat = *Impatiens* spp., Droq = *Droquetia iners*, Oenan = *Oenanthe procumbens*, C.Nya = *Carduus nyassanus*, S.Trich = *Senecio trichopterygius*, Crasso = *Crassocephalum ducis-aprutii*, Plect = *Plectranthus* spp., Stach = *Stachys aculeolata*, Solen = *Solenostemon sylvaticum*, Lap = *Laportea alatipes*, Steph = *Stephania abyssinica*, Tylo = *Tylophoropsis heterophylla*, P.Lind = *Peucedanum linderi*, Gynura = *Gynura ruwenzoriensis*, Urtic = *Urtica massaica*, L.gib = *Lobelia giberroa*, Hag = *Hagenia abyssinica*, Hyp = *Hypericum revolutum*,
1 = *Hypericum revolutum lvs, Helichryssum globosum, Hypericum peplidifolium.*

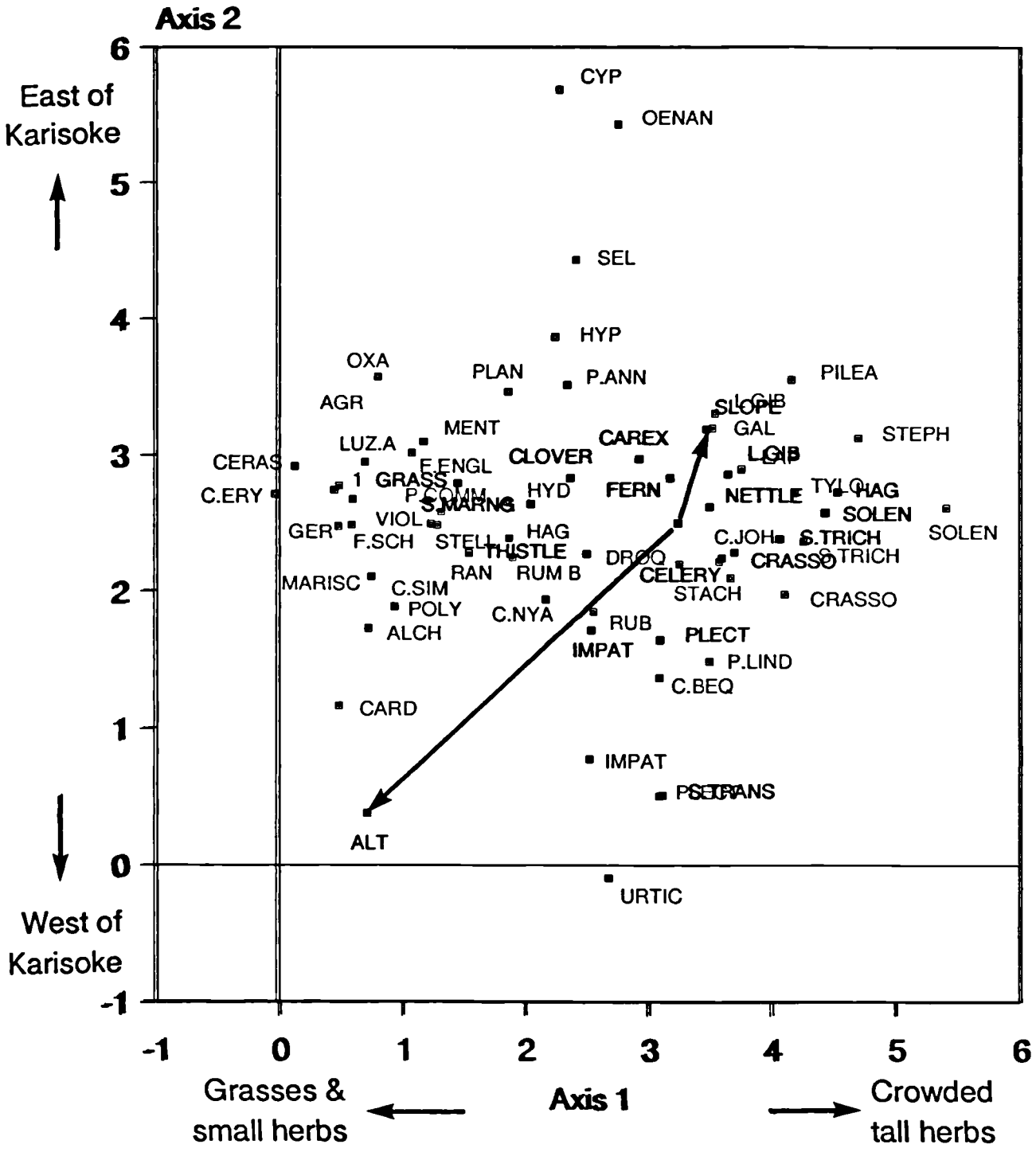
Vegetation types/Environmental variables:

Impat = *Impatiens* spp., Solen = *Solenostemon sylvaticum*, S.trich = *Senecio trichopterygius*, Hag = *Hagenia abyssinica*, Crasso = *Crassocephalum ducis-aprutii*, S.marng = *Senecio maranguensis*, Plect = *Plectranthus* spp., S.trans = *Senecio transmarinus*, L.gib = *Lobelia giberroa*, Alt = Altitude

Saddle


Axis 2
East of Karisoke
West of Karisoke
6
5
4
3
2
1
0
-1
-1
0
1
2
3
4
5
6
Grasses & small herbs
Axis 1
Crowded tall herbs
SLOPE
CAREX
CLOVER
L.GIB
GRASS
FERN
NETTLE
HAG
S.MARNG
SOLEN
S.TRICH
THISTLE
CRASSO
CELERY
PLECT
IMPAT
S.TRANS
ALT

Saddle


Axis 2
East of Karisoke
West of Karisoke
Axis 1
Grasses & small herbs
Crowded tall herbs
6
5
4
3
2
1
0
-1
-1
0
1
2
3
4
5
6
CYP
OENAN
SEL
HYP
OXA
PLAN
P.ANN
PILEA
AGR
SLOPE
GAL
MENT
LUZ.A
CAREX
STEPH
CERAS
CLOVER
F.ENGL
GRASS
C.ERY
HYD
FERN
NETTLE
HAG
SOLEN
VIOL
GER
F.SCH
STELL
HAG
C.JOH
S.TRICH
SOLEN
THISTLE
DROO
CRASSO
RAN
RUM B
CELERY
MARISC
C.SIM
STACH
CRASSO
POLY
C.NYA
RUB
ALCH
IMPAT
PLECT
P.LIND
C.BEQ
CARD
IMPAT
ALT
URTIC

Saddle

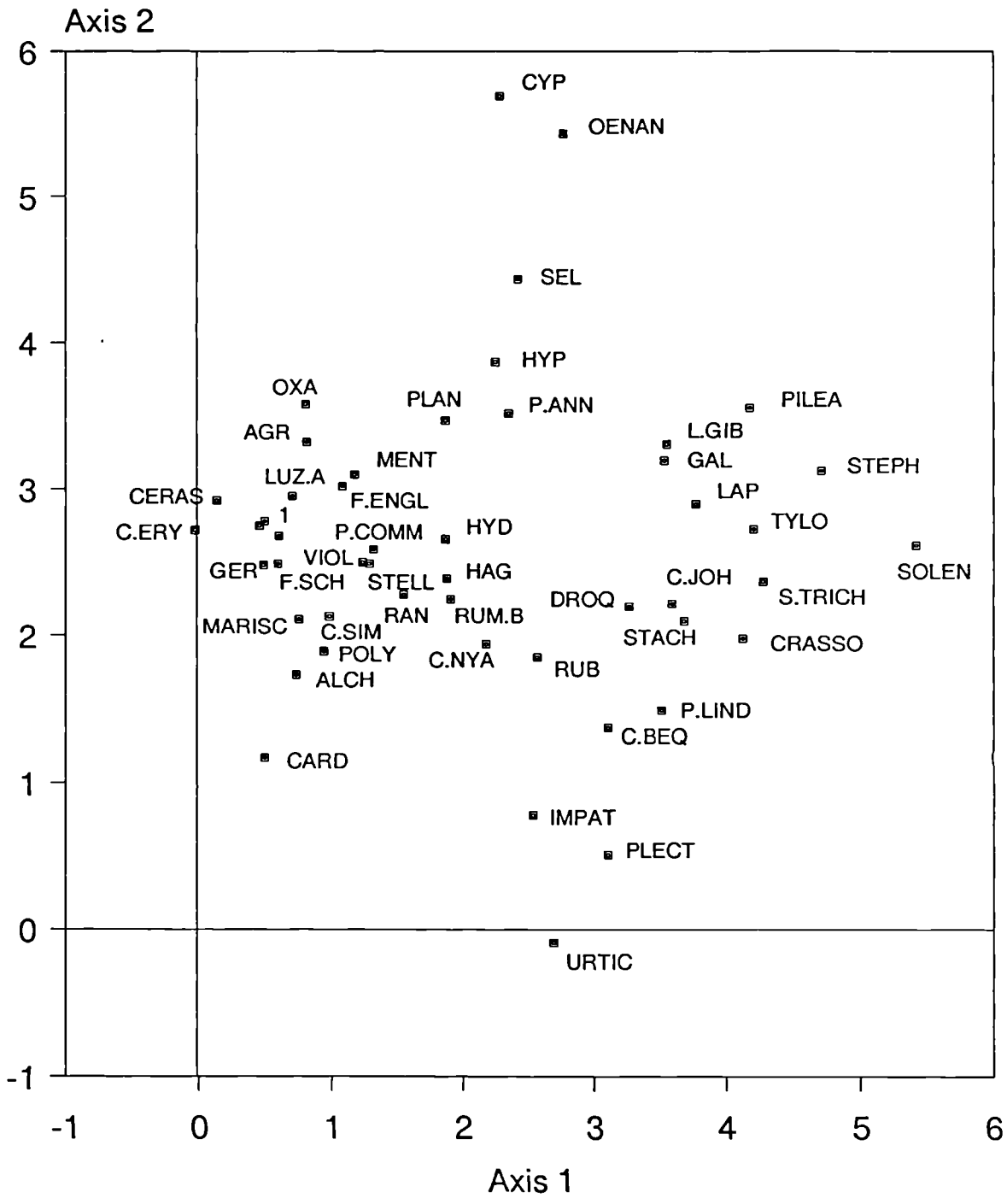

Axis 2
6
5
4
3
2
1
0
-1
-1
0
1
2
3
4
5
6
Axis 1
CYP
OENAN
SEL
HYP
OXA
PLAN
P.ANN
PILEA
AGR
L.GIB
MENT
GAL
STEPH
LUZ.A
CERAS
F.ENGL
LAP
1
C.ERY
P.COMM
HYD
TYLO
VIOL
GER
F.SCH
STELL
HAG
C.JOH
SOLEN
DROQ
S.TRICH
MARISC
C.SIM
RAN
RUM.B
STACH
CRASSO
POLY
C.NYA
RUB
ALCH
P.LIND
C.BEQ
CARD
IMPAT
PLECT
URTIC

Figure 2.11 Ordination of the Meadow community data. Axis one is a separation of plant species found at higher altitudes (on the right) from low altitudes although the cause of this may be due to other factors. Axis two separates those species found on waterlogged ground (at the top) from those on firm ground.

Key:

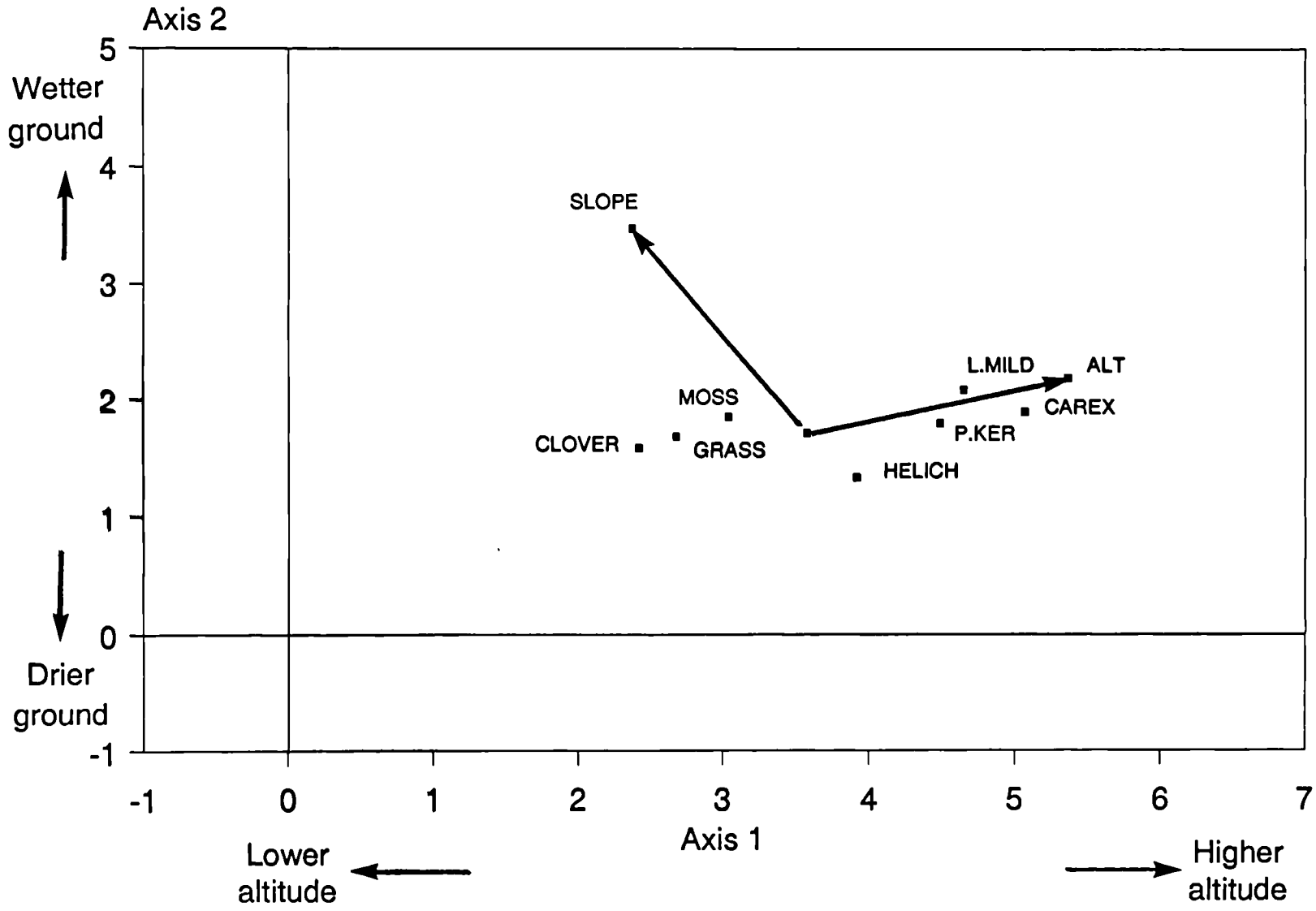
Plant species:

Agr = *Agrostis* spp., Des = *Deschampsia flexuosa*, C.ery = *Carex erythrorhiza*, C.sim = *Carex simensis*, C.Beq = *Carex bequaertii*, Luz.A = *Luzula abyssinica*, F.sch = *Festuca schimperiana*, Marisc = *Mariscus karisimbiensis*, Junc = *Juncus* spp., Panic = *Panicum striatissimum*, Isol = *Isolepis* spp., Lyco = *Lycopodium sauraurus*, Ceras = *Cerastium* spp., Card = *Cardamine obliqua*, Hyd = *Hydroctyle* spp., P.comm = *Parochetus communis*, Oxa = *Oxalis procumbens*, Viol = *Viola emminii*, Ment = *Mentha aquatica*, Ger = *Geranium arabicum*, Alch = *Alchemilla sps*, Alch.J = *Alchemilla johnstonii*, Poly = *Polygonum nepalense*, Rum.b = *Rumex bequaertii*, Stell = *Stellaria sennii*, Ran = *Ranunculus* spp., Gal = *Galium* spp., Sel = *Selaginella kraussiana*, Swer = *Swertia macrosepala*, H.pep = *Hypericum peplidifolium*, Trif = *Trifolium sps*, Helich = *Helichryssum globosum*, C.Nya = *Carduus nyassanus*, P.ker = *Peucedanum kerstenii*, L.mild = *Lobelia mildbraedii*, Hyp = *Hypericum revolutum*,

Vegetation types/Environmental variables:

P.Ker = *Peucedanum kerstenii*, Helich = *Helichryssum globosum*, L.mild = *Lobelia mildbraedii*, Alt = Altitude

Meadow


Axis 2
5
Wetter ground
4
3
2
1
0
Drier ground
-1
SLOPE
L.MILD
ALT
MOSS
CAREX
P.KER
CLOVER
GRASS
HELICH
-1
0
1
2
3
4
5
6
7
Axis 1
Lower altitude
Higher altitude

Meadow

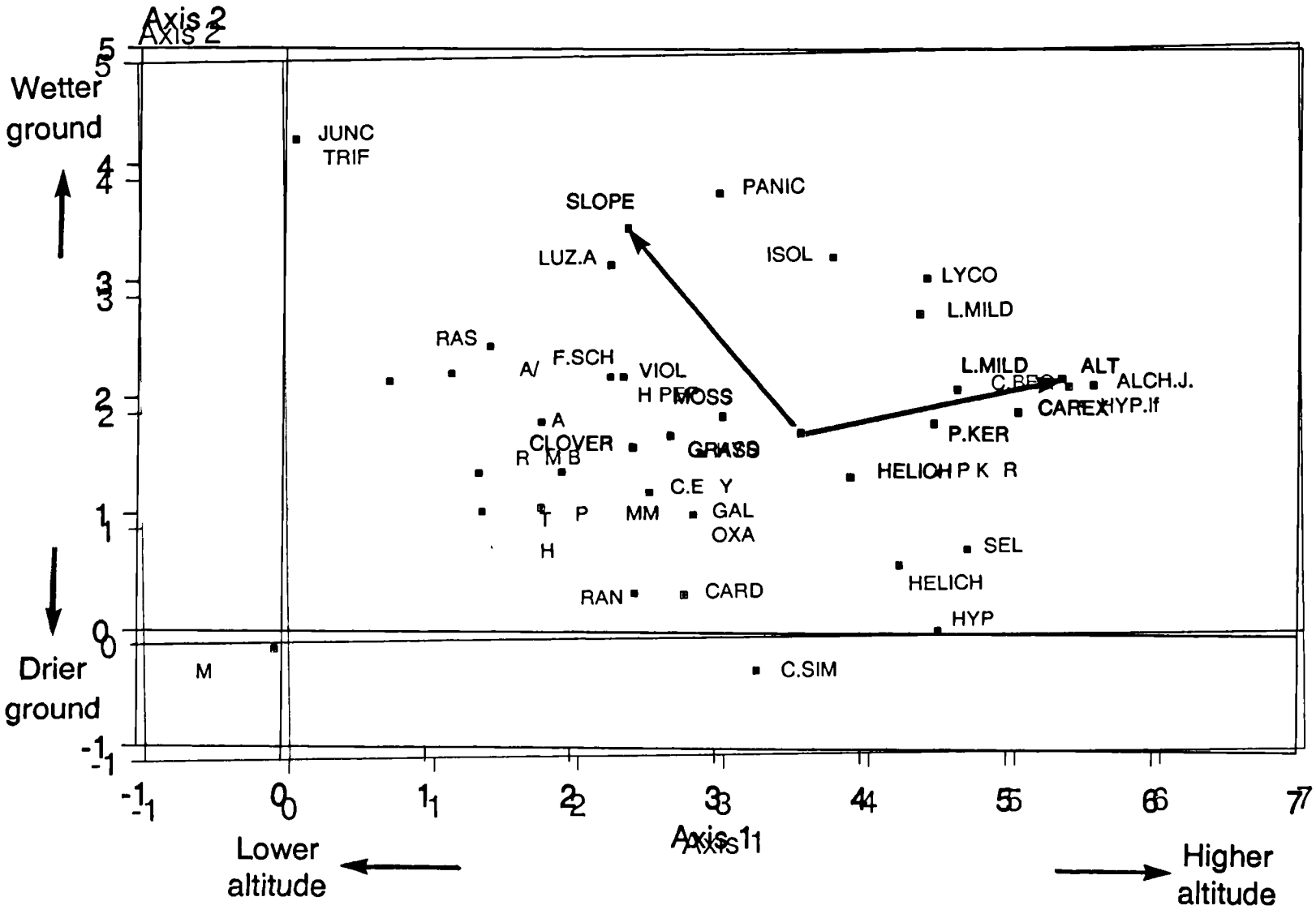

Axis 2
Wetter ground
Drier ground
JUNC TRIF
SLOPE
PANIC
LUZ.A
ISOL
LYCO
L.MILD
RAS
F.SCH
VIOL
L.MILD
ALT
ALCH.J.
CAREX
P.KER
CLOVER
HELICH
SEL
HELICH
RAN
CARD
HYP
C.SIM
M
Axis 1
Lower altitude
Higher altitude

Figure 2.12 Ordination of Herbaceous zone leaf mass data. Axis one separates the taller denser herbaceous areas on the right from the more open areas. Axis two is less clear but seems to separate those plants found on the slopes of Bisoke (at the bottom of the plot) from those plants found at the base of Bisoke.

Key:

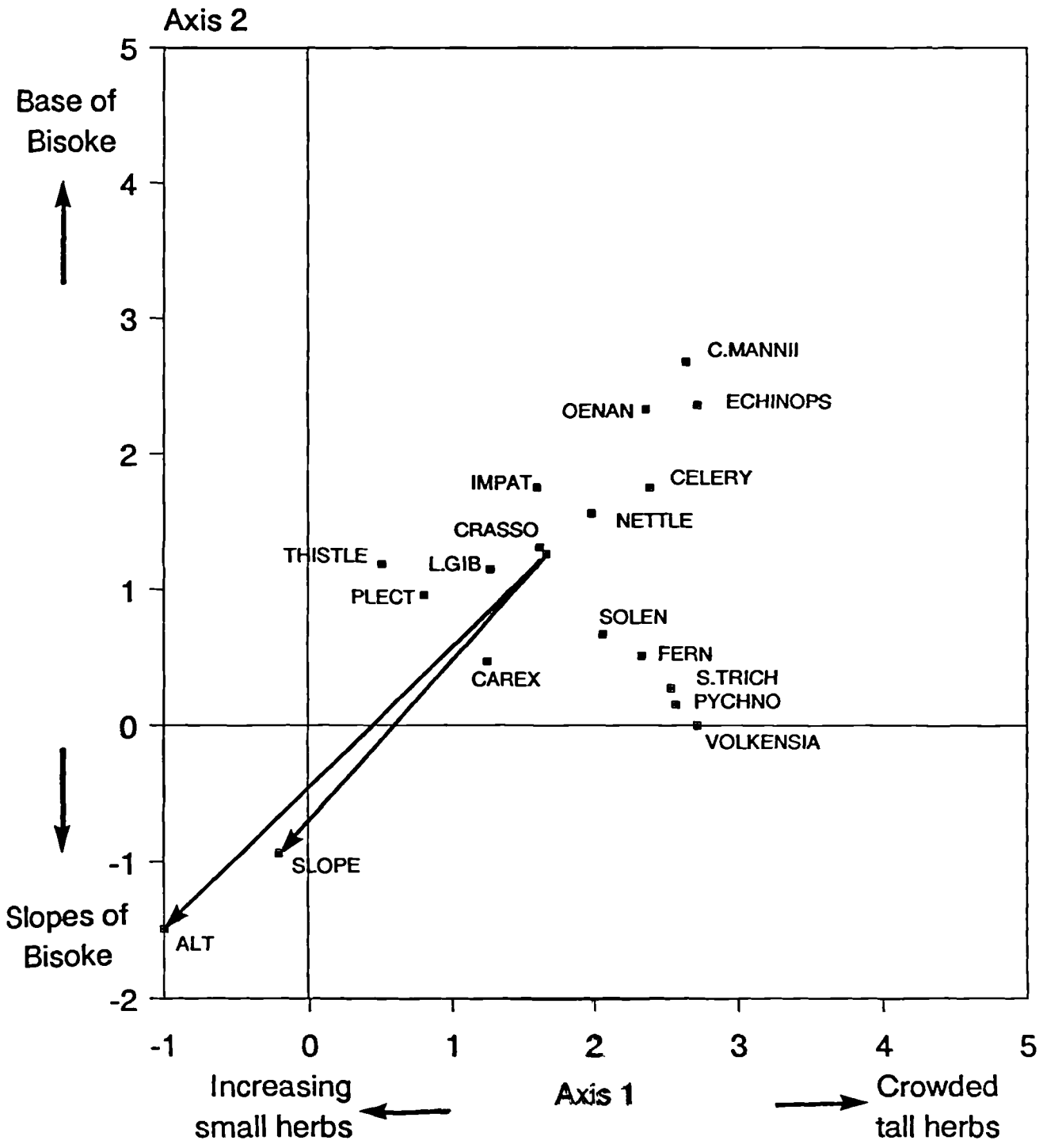
Plant species:

Agr = *Agrostis* spp., C.sim = *Carex simensis,* C.Beq = *Carex bequaertii*, F.engl = *Festuca engleri*, Ceras = *Cerastium* spp., Hyd = *Hydroctyle* spp., P.comm = *Parochetus communis*, Viol = *Viola emminii*, Alch = *Alchemilla* spp., Rum = *Rumex bequaertii*, Poly = *Polygonum nepalense*, Card = *Cardamine obliqua*, Stell = *Stellaria sennii*, Gal = *Galium* spp., Sel = *Selaginella kraussiana*, Pilea = *Pilea rivularis*, Impat = *Impatiens* spp., Droq = *Droquetia iners*, Oenan = *Oenanthe procumbens*, C.Nya = *Carduus nyassanus,* Echin = *Echinops hoelenii*, S.Trich = *Senecio trichopterygius*, S.tran = *Senecio transmarinus*, Crasso = *Crassocephalum ducis-aprutii*, Plect = *Plectranthus* spp., Stach = *Stachys aculeolata*, Solen = *Solenostemon sylvaticum*, Lap = *Laportea alatipes*, Steph = *Stephania abyssinica*, Zehn = *Zehneria* scabra, Tylo = *Tylophoropsis heterophylla*, P.Lind = *Peucedanum linderi*, Gynura = *Gynura ruwenzoriensis*, Urtic = *Urtica massaica*, L.gibb = *Lobelia giberroa*, Rub = *Rubus* spp.,

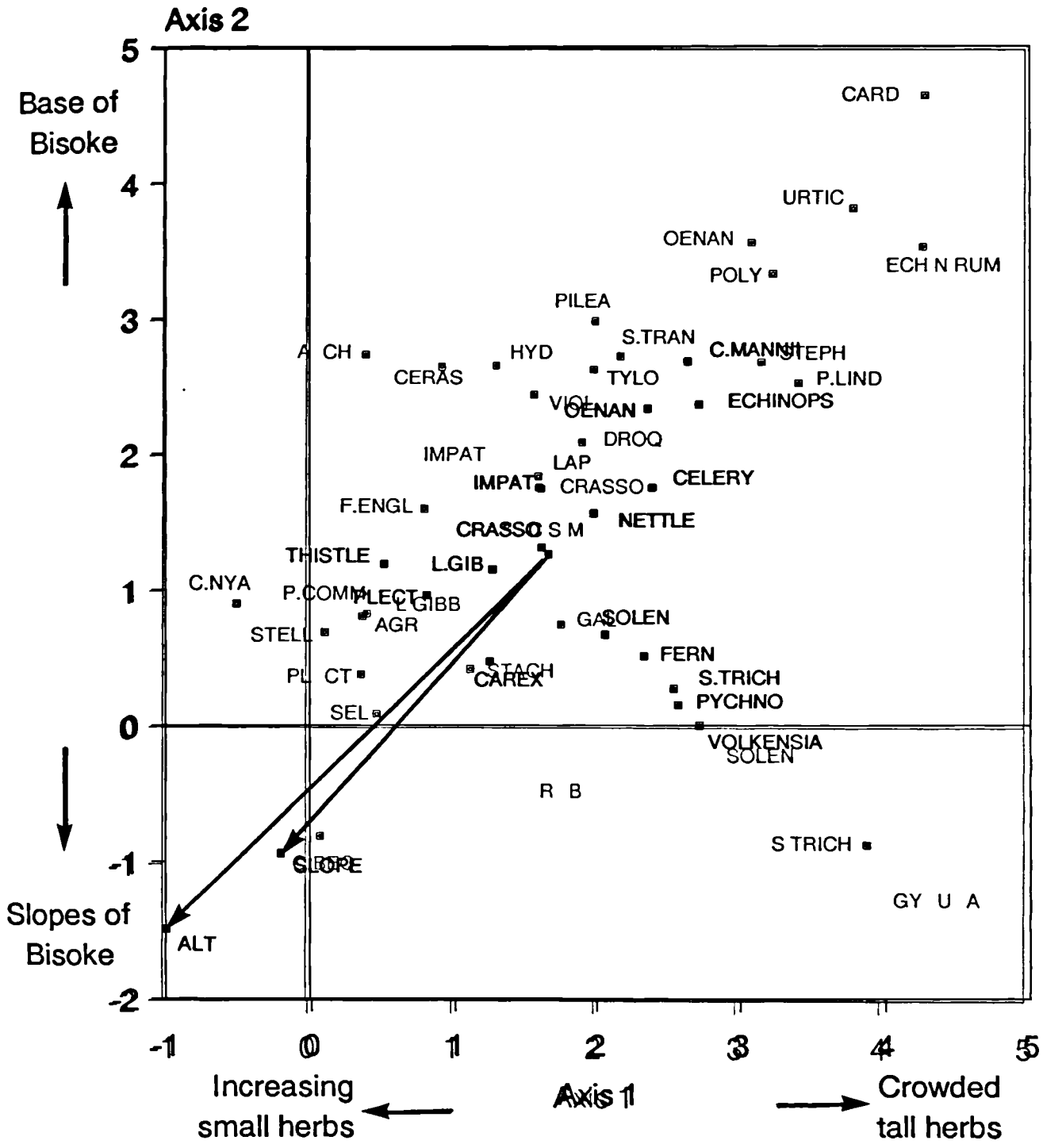
Vegetation types/Environmental variables:

Impat = *Impatiens* spp., Solen = *Solenostemon sylvaticum*, S.trich = *Senecio trichopterygius*, Crasso = *Crassocephalum ducis-aprutii,* Plect = *Plectranthus* spp., Pychno = *Pychnostachys goetzenii*, Volkensia = *Volkensia ruwenzoriensis*, C.mannii = *Crassocephalum mannii*, L.gib = *Lobelia giberroa*, Alt = Altitude

Herbaceous


Axis 2
Base of Bisoke
Slopes of Bisoke
Axis 1
Increasing small herbs
Crowded tall herbs
5
4
3
2
1
0
-1
-2
-1
0
1
2
3
4
5
C.MANNII
ECHINOPS
OENAN
CELERY
IMPAT
NETTLE
CRASSO
THISTLE
L.GIB
PLECT
SOLEN
FERN
CAREX
S.TRICH
PYCHNO
VOLKENSIA
SLOPE
ALT

Herbaceous


Axis 2
Base of Bisoke
Slopes of Bisoke
Axis 1
Increasing small herbs
Crowded tall herbs
CARD
URTIC
OENAN
ECH N RUM
POLY
PILEA
S.TRAN
C.MANNI
STEPH
HYD
CERAS
TYLO
P.LIND
VIOL
OENAN
ECHINOPS
DROQ
IMPAT
LAP
IMPAT
CRASSO
CELERY
F.ENGL
NETTLE
CRASSO
S M
THISTLE
L.GIB
C.NYA
P.COMM
PLECT
L.GIBB
AGR
STELL
GA
SOLEN
FERN
PL CT
STACH
CAREX
S.TRICH
PYCHNO
SEL
VOLKENSIA
SOLEN
R B
S TRICH
GY U A
ALT

Herbaceous

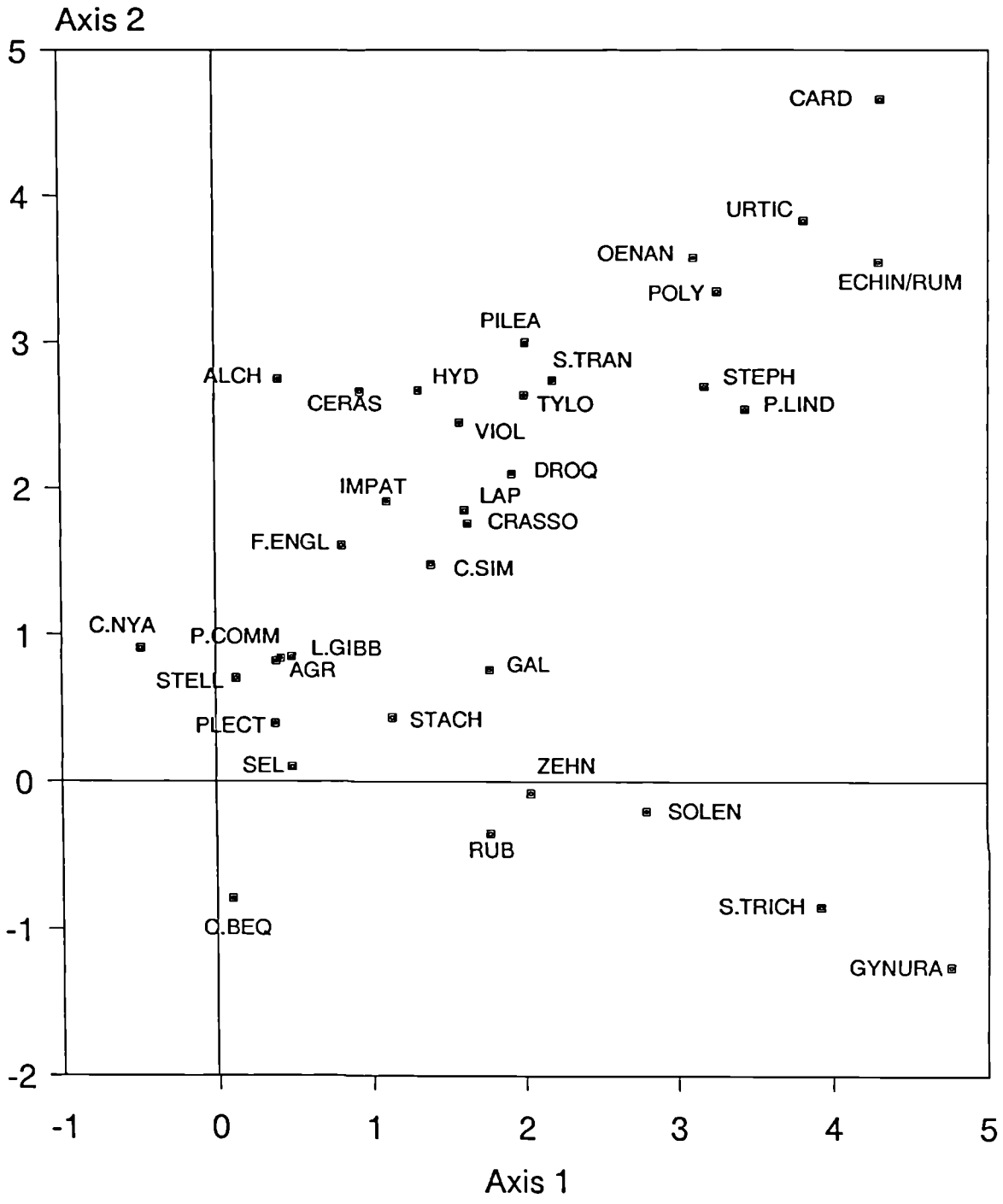

Axis 2
5
4
3
2
1
0
-1
-2
-1
0
1
2
3
4
5
Axis 1
CARD
URTIC
OENAN
ECHIN/RUM
POLY
PILEA
S.TRAN
ALCH
HYD
STEPH
CERAS
TYLO
P.LIND
VIOL
DROQ
IMPAT
LAP
CRASSO
F.ENGL
C.SIM
C.NYA
P.COMM
L.GIBB
AGR
GAL
STELL
PLECT
STACH
SEL
ZEHN
SOLEN
RUB
S.TRICH
C.BEQ
GYNURA

Figure 2.13 Ordination of the leaf mass data for the Brush Ridge habitat. Axis one separates the more open grassy areas (on the right) from the more densely vegetated areas. Axis two separates the plants found near the base of Bisoke (at the top) from those found higher up.

Key:

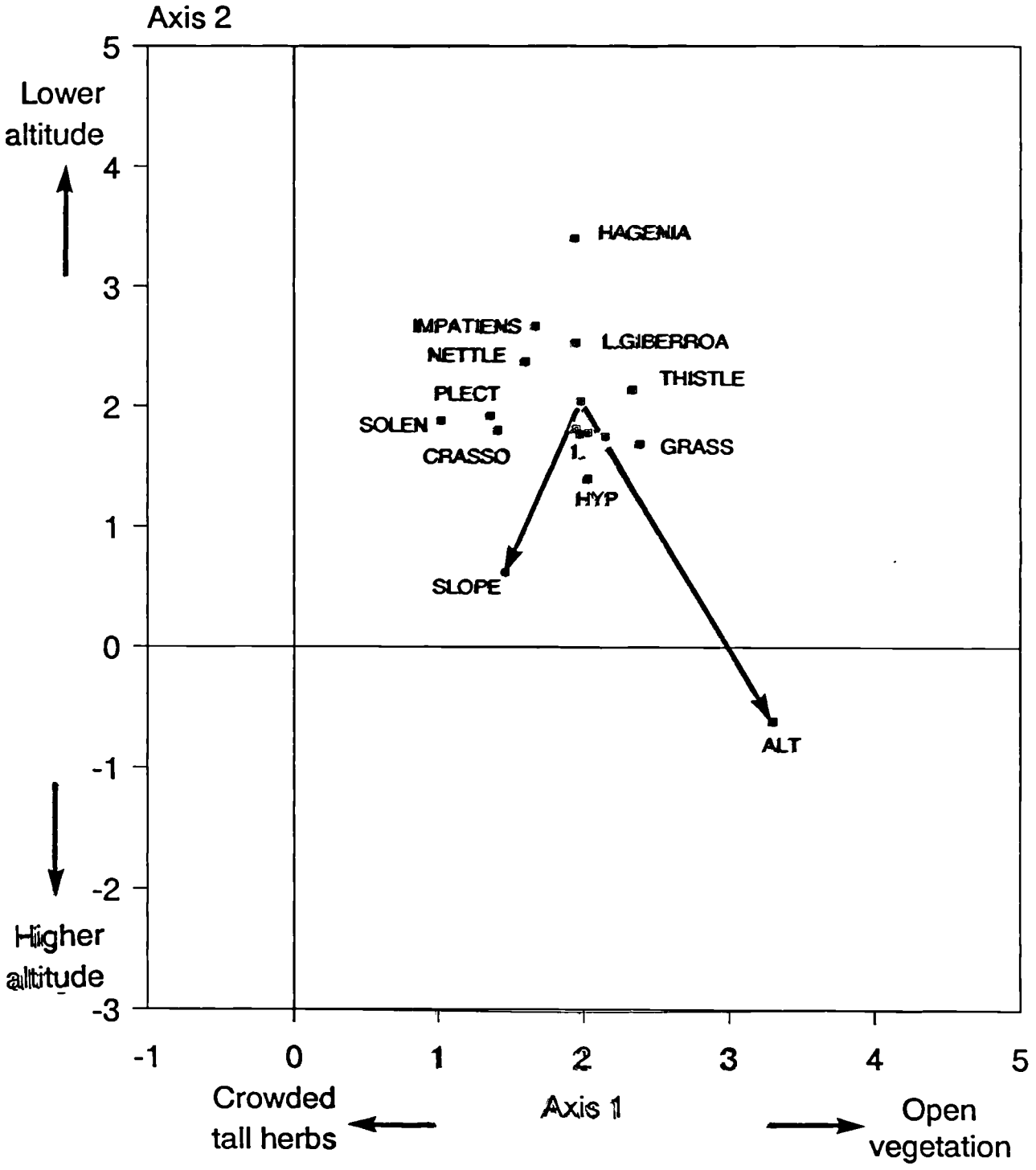
Plant species:

Agr = *Agrostis* spp., C.sim = *Carex simensis,* C.joh = *Carex johnstonii*, Luz.A = *Luzula abyssinica*, P.ann = *Poa annua*, F.engl = *Festuca engleri*, F.sch = *Festuca schimperiana*, Card = *Cardamine obliqua*, Hyd = *Hydroctyle* spp., P.comm = *Parochetus communis*, Viol = *Viola emminii*, Ment = *Mentha aquatica*, Alch = *Alchemilla* spp., Ran = *Ranunculus* spp., Gal = *Galium* spp., Sel = *Selaginella kraussiana*, Pilea = *Pilea rivularis*, Impat = *Impatiens* spp., Droq = *Droquetia iners*, C.Nya = *Carduus nyassanus,* S.Tri = *Senecio trichopterygius*, Crass = *Crassocephalum ducis-aprutii*, Plec = *Plectranthus* spp., Stach = *Stachys aculeolata*, Solen = *Solenostemon sylvaticum*, Lap = *Laportea alatipes*, Steph = *Stephania abyssinica*, Tylo = *Tylophoropsis heterophylla*, P.Lin = *Peucedanum linderi*, Gynura = *Gynura ruwenzoriensis*, L.stu = *Lobelia stuhlmannii*, L.gib = *Lobelia giberroa*, Rub = *Rubus* spp., Hag = *Hagenia abyssinica*, Hyp = *Hypericum revolutum*,

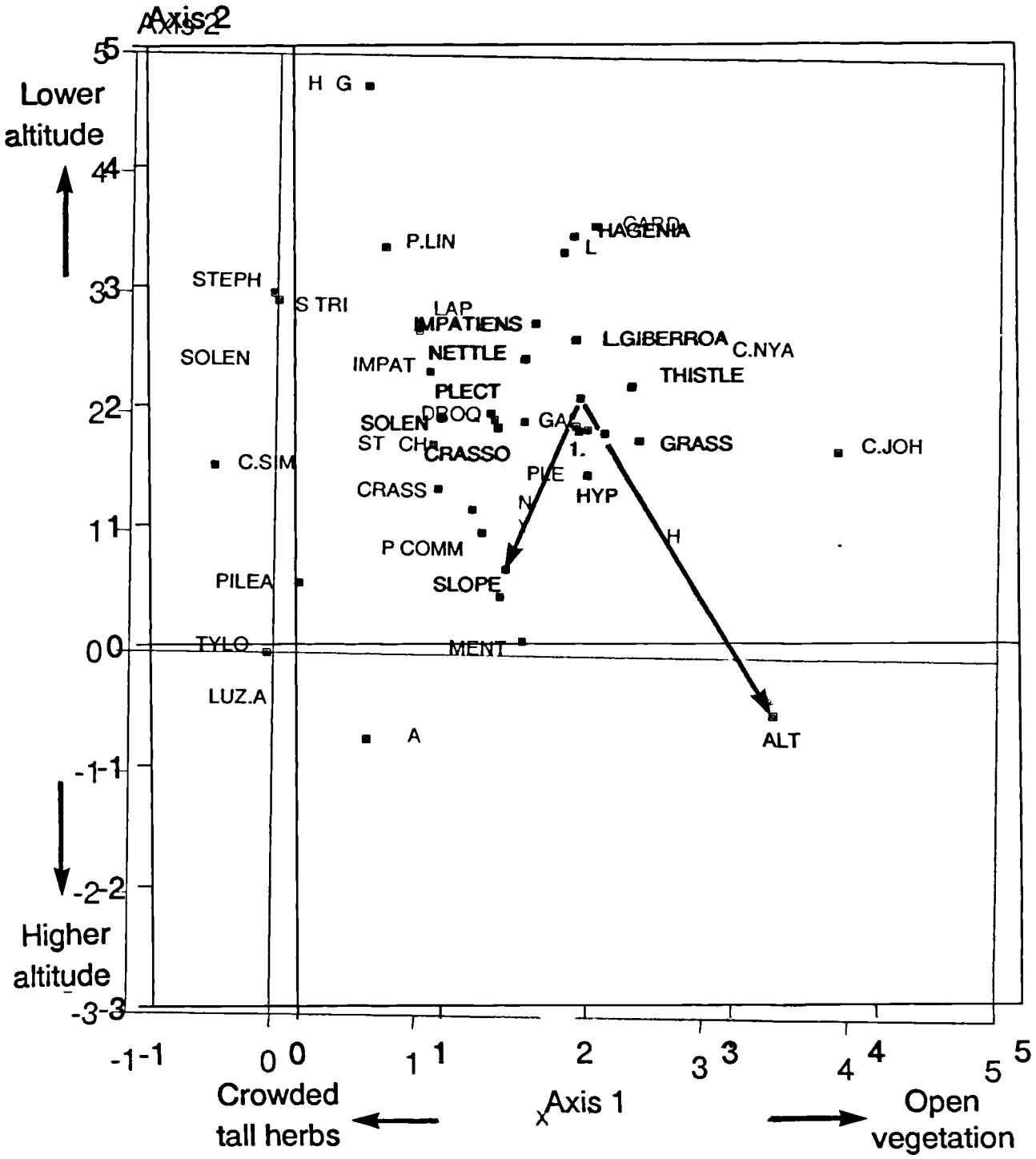
Vegetation types/Environmental variables:

Solen = *Solenostemon sylvaticum*, Crasso = *Crassocephalum ducis-aprutii,* Plect = *Plectranthus* spp., L.giberroa = *Lobelia giberroa*, Alt = Altitude
1 = *Senecio mariettae, Conyza adolfi-frederici,* Fern, Clover.

Brush Ridge


Axis 2
5
Lower
altitude
4
3
2
1
0
-1
-2
Higher
altitude
-3
HAGENIA
IMPATIENS
NETTLE
L.GIBERROA
THISTLE
PLECT
SOLEN
CRASSO
GRASS
HYP
SLOPE
ALT
-1
0
1
2
3
4
5
Crowded
tall herbs
Axis 1
Open
vegetation

Brush Ridge


Axis 2
Lower altitude
Higher altitude
Axis 1
Crowded tall herbs
Open vegetation
H G
P.LIN
L
HAGENIA
STEPH
S TRI
LAP
IMPATIENS
L.GIBERROA
C.NYA
SOLEN
IMPAT
NETTLE
THISTLE
PLECT
SOLEN
DROQ
GA
ST CH
CRASSO
GRASS
C.JOH
C.SIM
CRASS
PLE
HYP
P COMM
PILEA
SLOPE
TYLO
MENT
LUZ.A
A
ALT

Brush Ridge

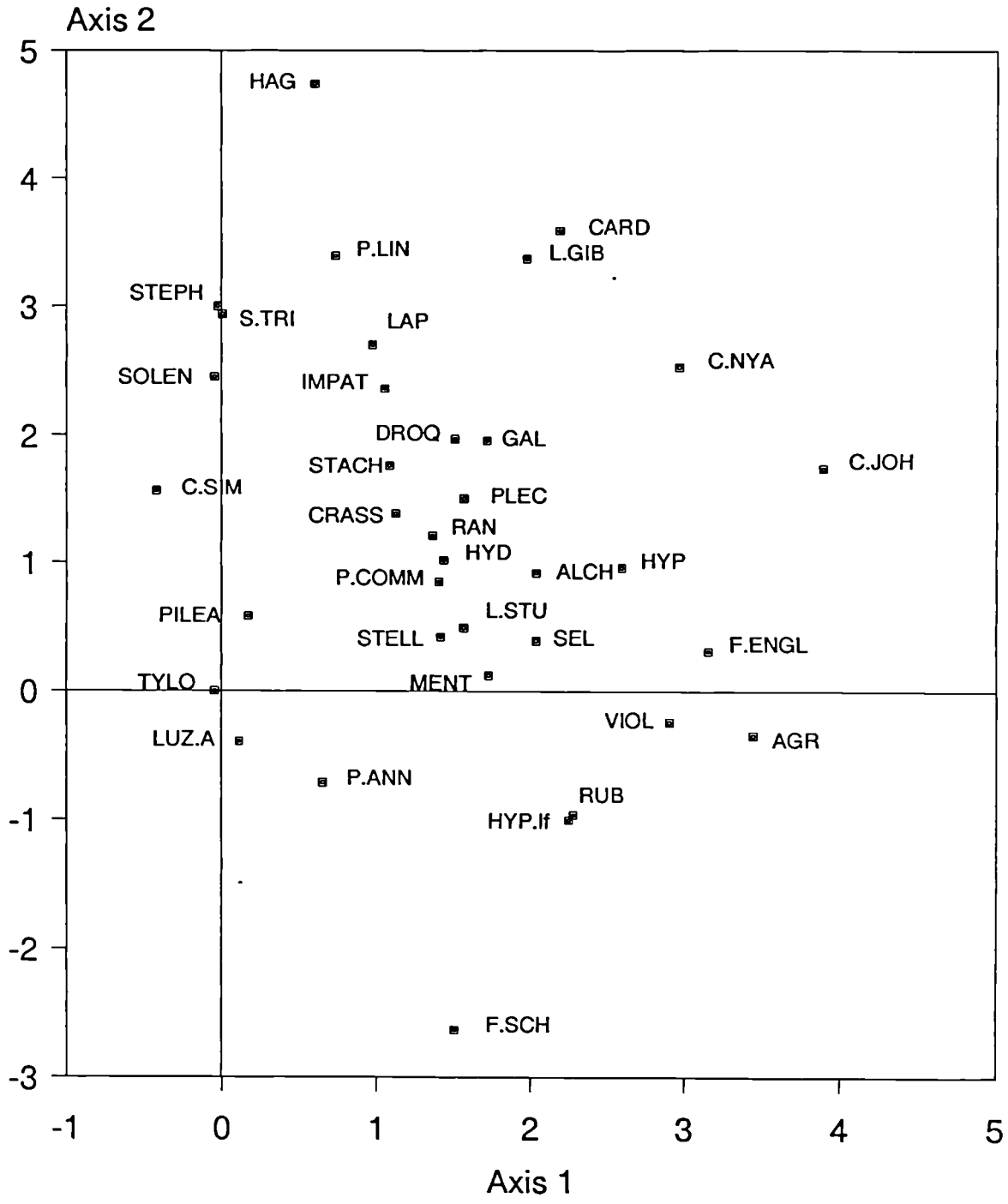

Axis 2
5
4
3
2
1
0
-1
-2
-3
HAG
CARD
P.LIN
L.GIB
STEPH
S.TRI
LAP
C.NYA
SOLEN
IMPAT
DROQ
GAL
C.JOH
STACH
C.SIM
PLEC
CRASS
RAN
HYD
HYP
P.COMM
ALCH
PILEA
L.STU
STELL
SEL
F.ENGL
TYLO
MENT
VIOL
LUZ.A
AGR
P.ANN
RUB
HYP.lf
F.SCH
-1
0
1
2
3
4
5
Axis 1

Figure 2.14 Ordination of the leaf mass data for the Giant *Lobelia* zone. Axis one separates the grassland communities (on the left) from the more wooded regions. Axis two seems to separate those plants found near the Brush ridge zone (at the top) from those found nearer the alpine zone.

Key:

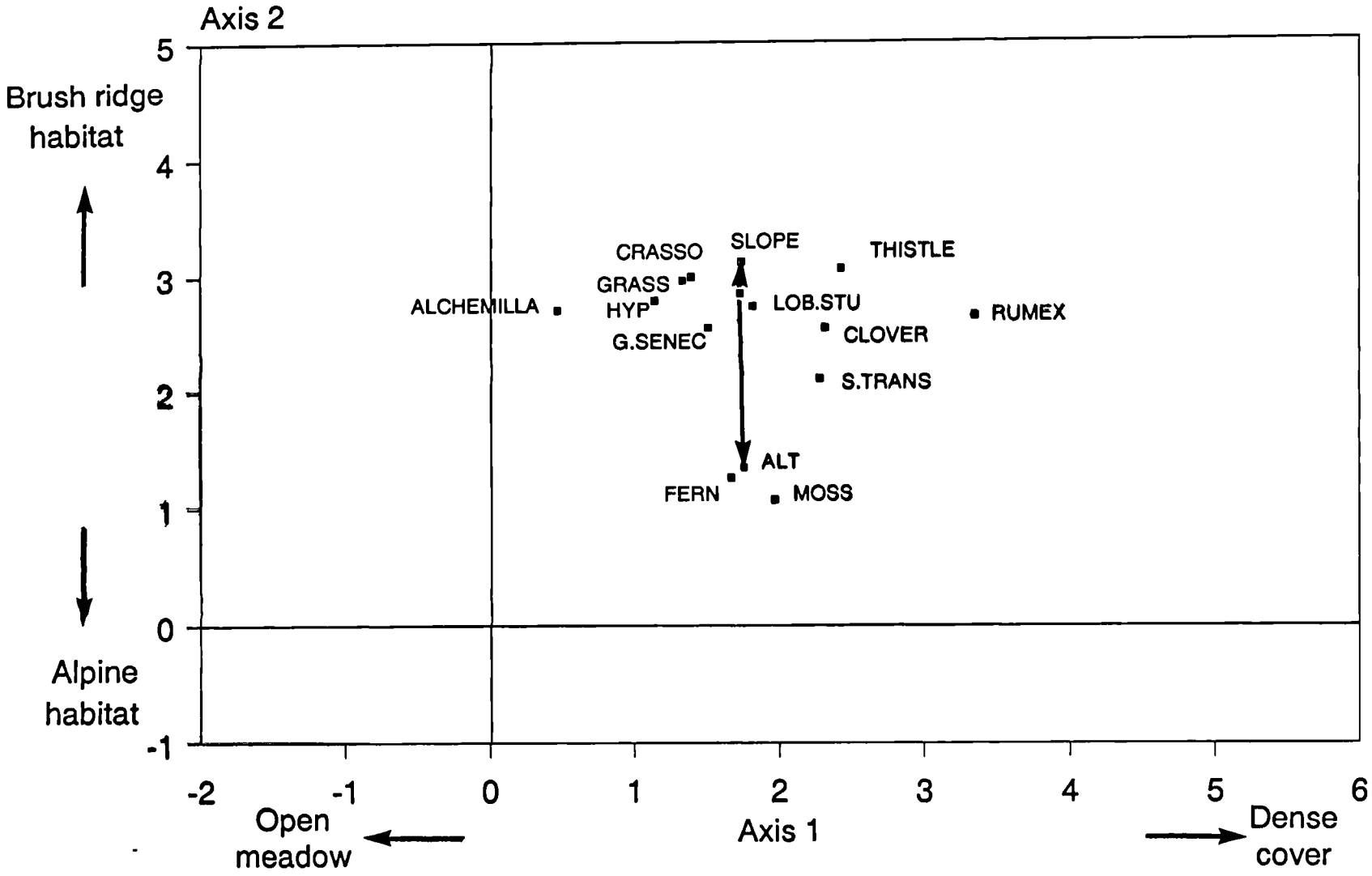
Plant species:

Agr = *Agrostis* spp., C.ery = *Carex erythrorhiza*, C.sim = *Carex simensis,* C.joh = *Carex johnstonii*, Luz.J = *Luzula johnstonii*, Luz.A = *Luzula abyssinica*, P.ann = *Poa annua*, F.engl = *Festuca engleri*, F.sch = *Festuca schimperiana*, Ceras = *Cerastium* spp., Hyd = *Hydroctyle* spp., P.comm = *Parochetus communis*, Ment = *Mentha aquatica*, Viol = *Viola emminii*, Alch.J = *Alchemilla johnstonii*, Alch = *Alchemilla* spp., Poly = *Polygonum nepalense*, Rum.r = *Rumex ruwenzoriense*, Stell = *Stellaria sennii*, Swer = *Swertia macrosepals*, Gal = *Galium* spp., Sel = *Selaginella kraussiana*, P.ker = *Peucedanum kerstenii*, Pilea = *Pilea rivularis*, Impat = *Impatiens* spp., C.Nya = *Carduus nyassanus,* Crass = *Crassocephalum ducis-aprutii*, Stach = *Stachys aculeolata*, Lap = *Laportea alatipes*, Rub = *Rubus* spp., L.stu = *Lobelia stuhlmannii*, G.sen = *Senecio johnstonii*, Hyp = *Hypericum revolutum*,

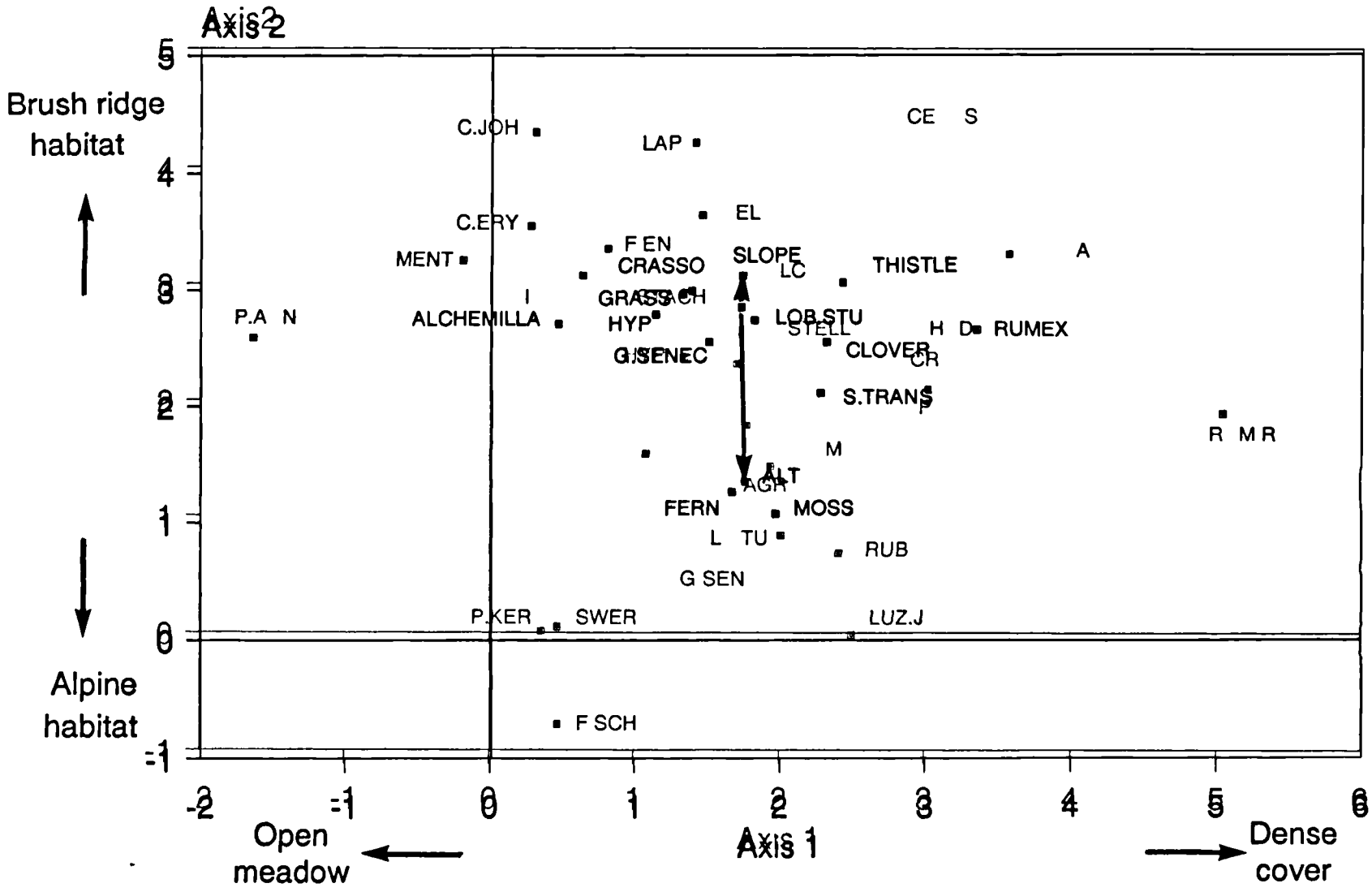
Vegetation types/Environmental variables:

Alchemilla = *Alchemilla johnstonii*, S.trans = *Senecio transmarinus*, Crasso = *Crassocephalum ducis-aprutii,* Lob.stu = *Lobelia stuhlmannii*, G.Senec = *Senecio johnstonii*, Hyp = *Hypericum revolutum*, Alt = Altitude

Giant Lobelia



Giant Lobelia



Giant Lobelia

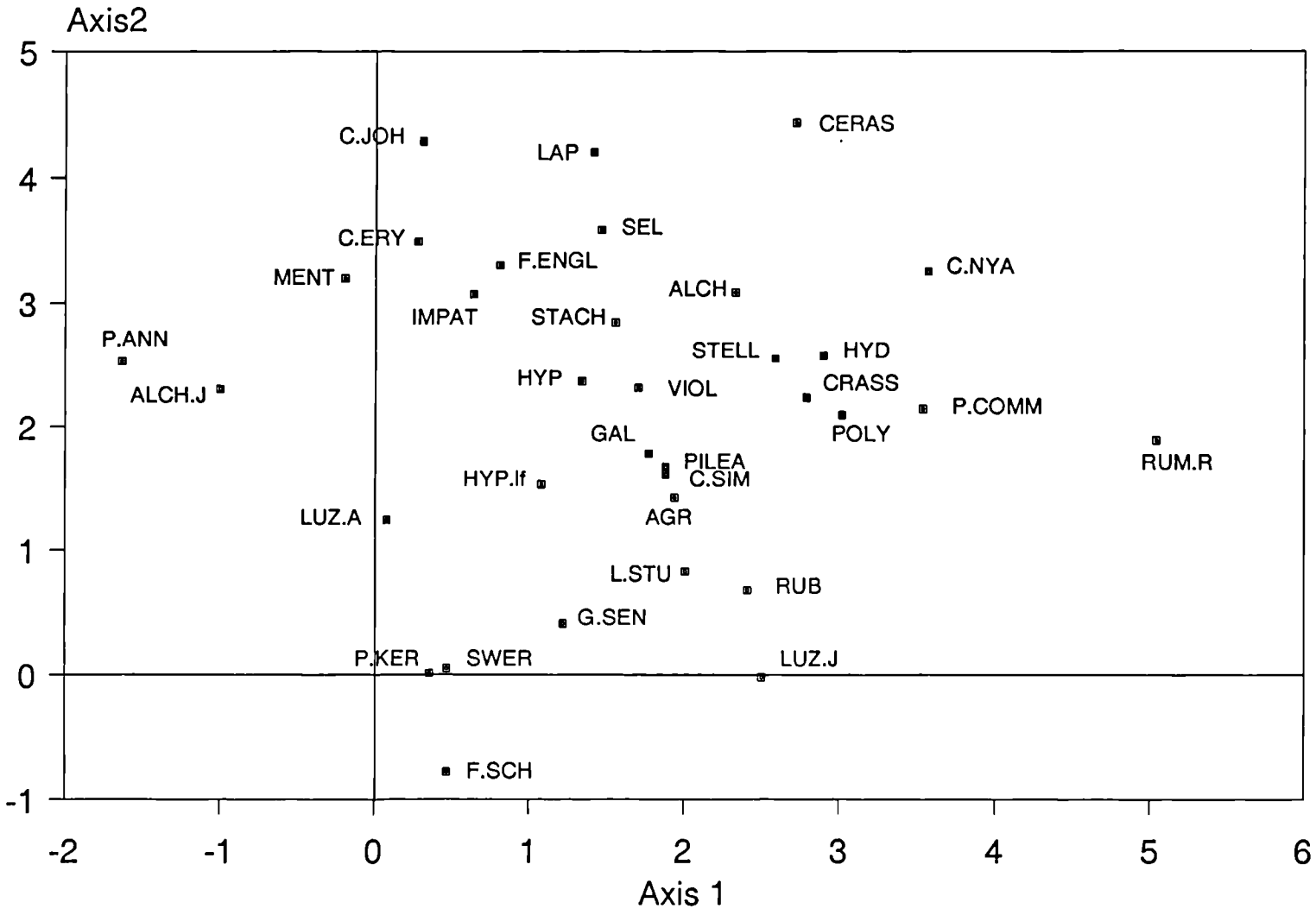


Figure 2.15 Ordination of the Alpine leaf mass data. Axis one separates the denser, wetter regions (on the right) from the more open grassy areas. Axis two is unclear but may be due to soil depth because many of the plant species at the top of the plot were found near scree slopes where the soil is shallow.

Key:

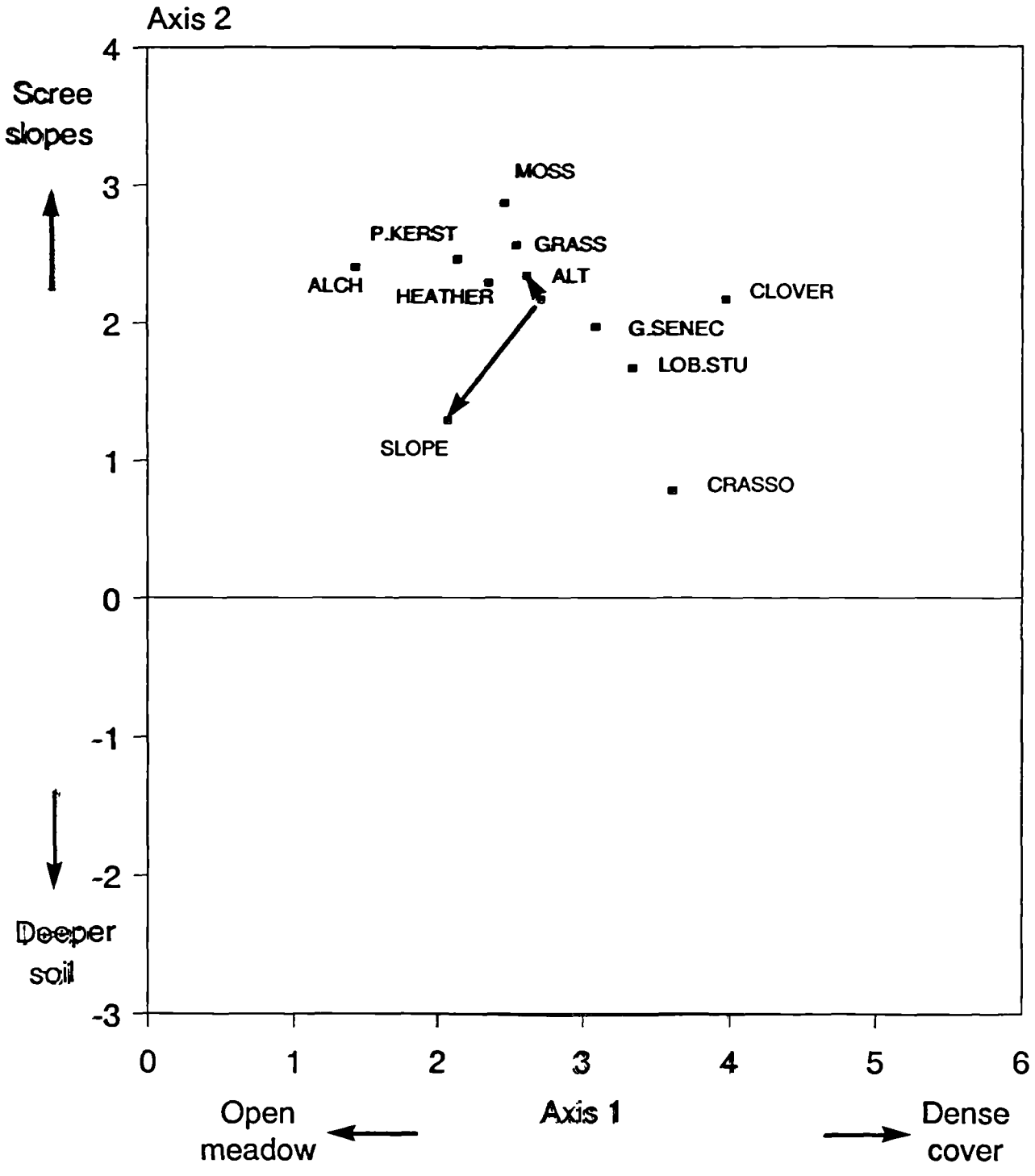
Plant species:

Agr = *Agrostis* spp.s, C.ery = *Carex erythrorhiza*, C.sim = *Carex simensis*, C.joh = *Carex johnstonii*, Luz.A = *Luzula abyssinica*, Luz.J = *Luzula johnstonii*, Isol = *Isolepis* spp., P.ann = *Poa annua*, F.Engl = *Festuca engleri*, F.sch = *Festuca schimperiana*, Ceras = *Cerastium* spp., Card = *Cardamine obliqua*, Hyd = *Hydroctyle* spp., Viol = *Viola emminii*, Alch.J = *Alchemilla johnstonii*, Alch = *Alchemilla* spp., Swer = *Swertia macrosepala*, S.sab = *Senecio sabinjoensis*, Stell = *Stellaria sennii*, Gal = *Galium* spp., Pilea = *Pilea rivularis*, C.Nya = *Carduus nyassanus*; P.ker = *Peucedanum kerstenii*, Crasso = *Crassocephalum ducis-aprutii*, Stach = *Stachys aculeolata*, Lyc = *Lycopodium sauraurus*, L.stu = *Lobelia stuhlmannii*, G.sen = *Senecio johnstonii*, Rub = *Rubus* spp., Hyp = *Hypericum revolutum*,

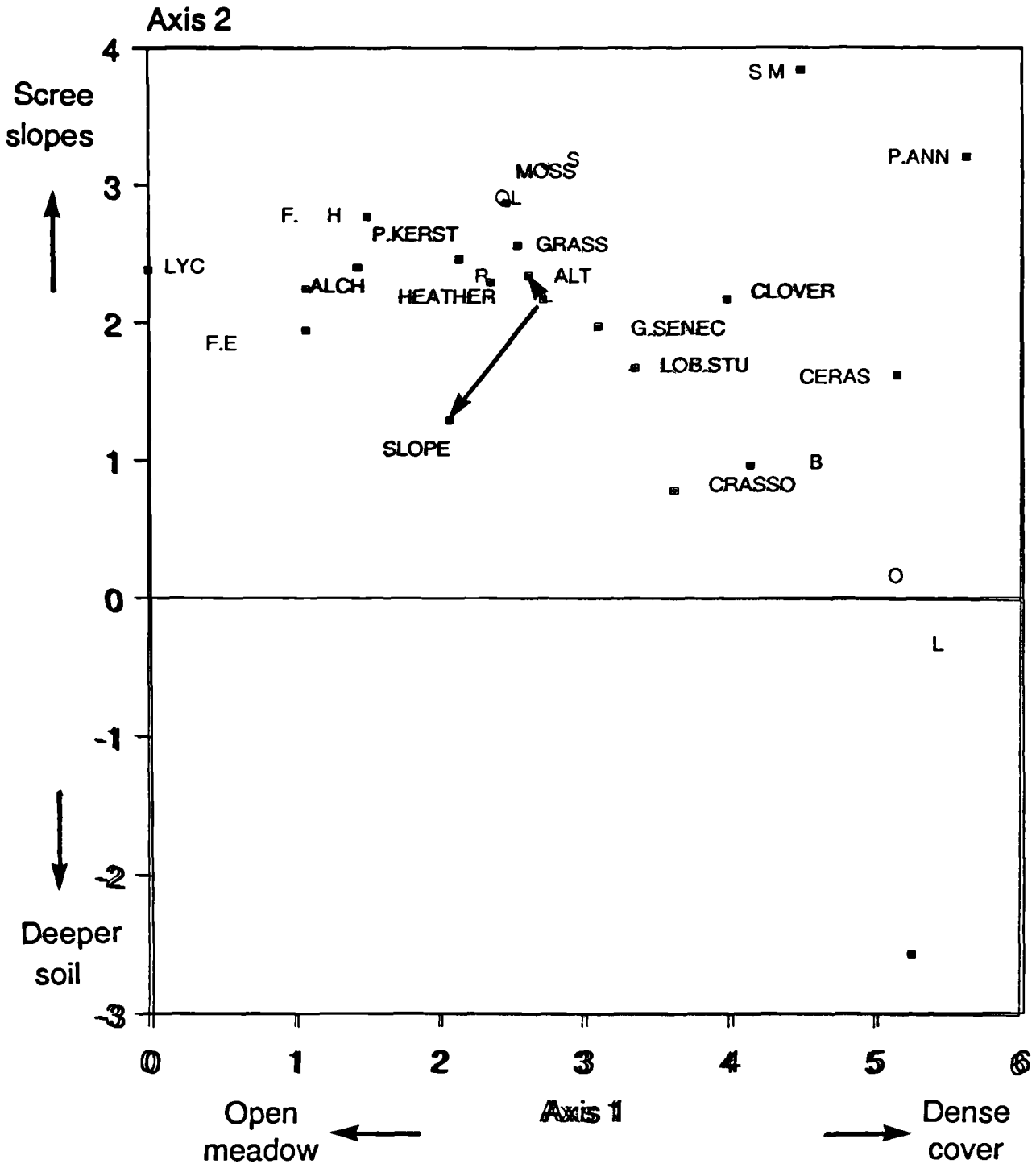
Vegetation types/Environmental variables:

Alch = *Alchemilla johnstonii*, G.Senec = *Senecio johnstonii*, P.kerst = *Peucedanum kerstenii*, Crasso = *Crassocephalum ducis-aprutii*, Lob.stu = *Lobelia stuhlmannii*, Alt = Altitude

Alpine


Axis 2
Scree slopes
Deeper soil
MOSS
P.KERST
GRASS
ALCH
HEATHER
ALT
CLOVER
G.SENEC
LOB.STU
SLOPE
CRASSO
4
3
2
1
0
-1
-2
-3
0
1
2
3
4
5
6
Open meadow
Axis 1
Dense cover

Alpine


Axis 2
Scree slopes
Deeper soil
Open meadow
Axis 1
Dense cover
4
3
2
1
0
-1
-2
-3
0
1
2
3
4
5
6
S M
P.ANN
MOSS
S
QL
F. H
P.KERST
GRASS
LYC
ALCH
R
ALT
HEATHER
CLOVER
F.E
G.SENEC
LOB.STU
CERAS
SLOPE
B
CRASSO
O
L

Alpine

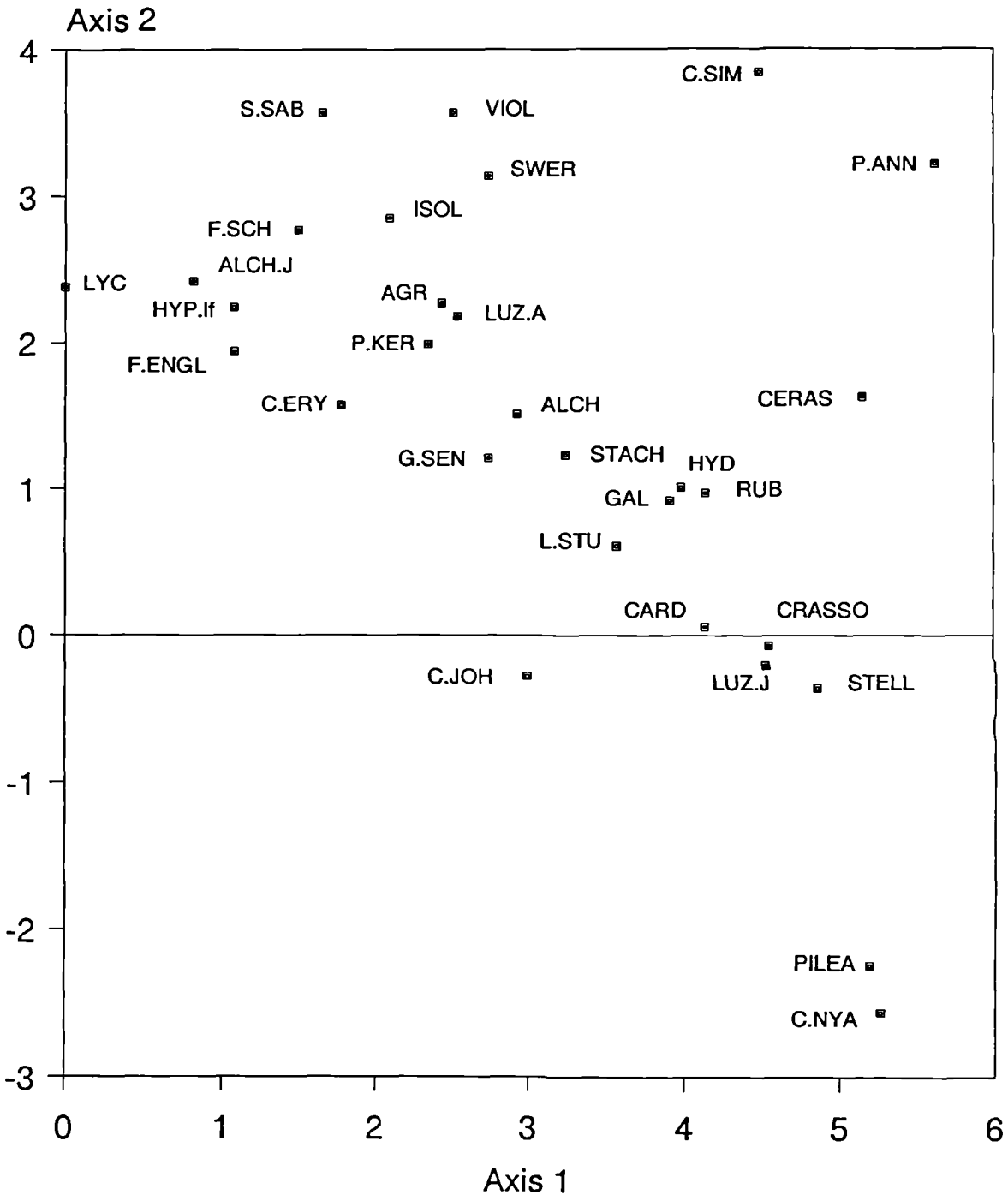

Axis 2
4
3
2
1
0
-1
-2
-3
0
1
2
3
4
5
6
Axis 1
C.SIM
S.SAB
VIOL
SWER
P.ANN
ISOL
F.SCH
ALCH.J
LYC
AGR
HYP.lf
LUZ.A
P.KER
F.ENGL
C.ERY
ALCH
CERAS
G.SEN
STACH
HYD
GAL
RUB
L.STU
CARD
CRASSO
C.JOH
LUZ.J
STELL
PILEA
C.NYA

Figure 2.16 Ordination of the Karisimbi meadows leaf mass data. Axis one separates the open grassy meadows (on the right) from areas with more cover. Axis two is unclear but may separate those plants that are found on wetter ground (at the bottom) from those in drier areas.

Key:

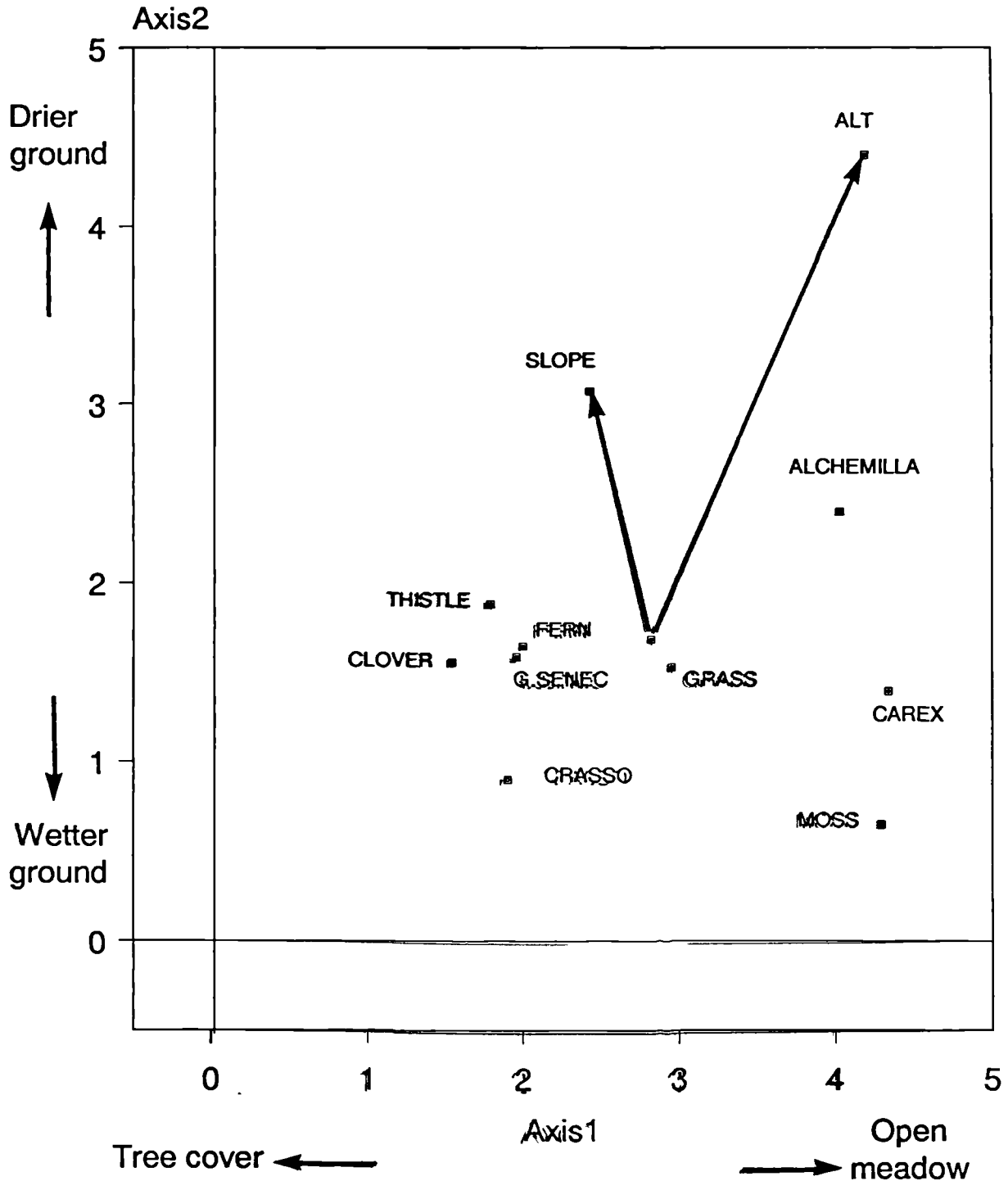
Plant species:

Agr = *Agrostis* spp., C.ery = *Carex erythrorhiza*, C.sim = *Carex simensis*, C.Beq = *Carex bequaertii*, Panic = *Panicum striatissimum*, Isol = *Isolepis* spp., Luz.A = *Luzula abyssinica*, Luz.J = *Luzula johnstonii*, P.ann = *Poa annua*, F.engl = *Festuca engleri*, F.sch = *Festuca schimperiana*, Ceras = *Cerastium* spp., Hyd = *Hydroctyle* spp., P.comm = *Parochetus communis*, Oxal = *Oxalis procumbens*, Viol = *Viola emminii*, Ment = *Mentha aquatica*, Ger = *Geranium arabicum*, Alch = *Alchemilla* spp., Alch.J = *Alchemilla johnstonii*, H.pep = *Hypericum peplidifolium*, Stel = *Stellaria sennii*, Ran = *Ranunculus* spp., Gal = *Galium* spp., S.sab = *Senecio sabinjoensis*, Swer = *Swertia macrosepala*, Sel = *Selaginella kraussiana*, Pil = *Pilea rivularis*, C.Nya = *Carduus nyassanus*, Crass = *Crassocephalum ducis-aprutii*, Stach = *Stachys aculeolata*, L.stu = *Lobelia stuhlmannii*, Rub = *Rubus* spp., G.sen = *Senecio johnstonii*, Hyp = *Hypericum revolutum*,

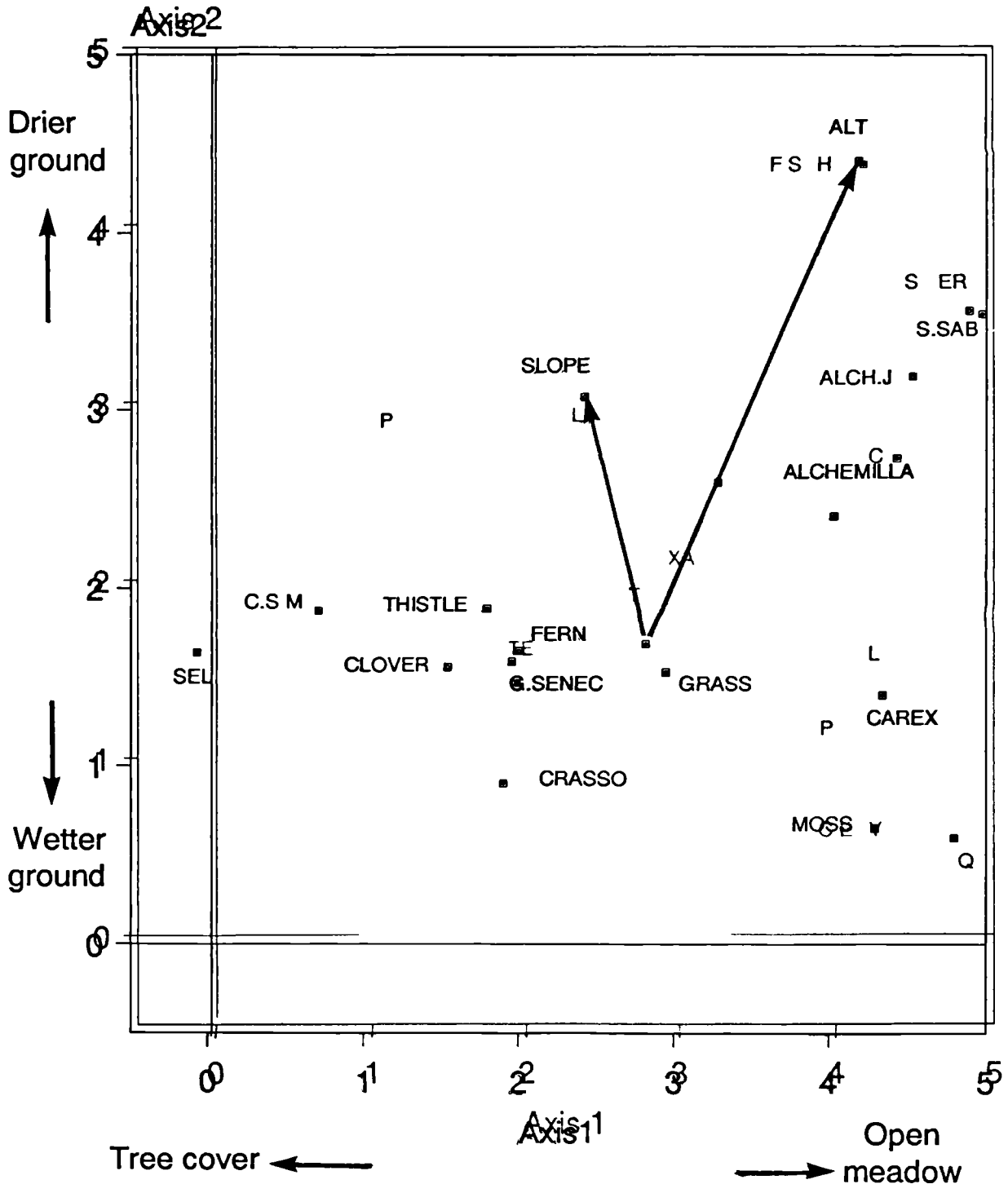
Vegetation types/Environmental variables:

Alchemilla = *Alchemilla johnstonii*, G.senec = *Senecio johnstonii*, Crasso = *Crassocephalum ducis-aprutii*, Alt = Altitude

Karisimbi meadows



Karisimbi meadows



Karisimbi meadows

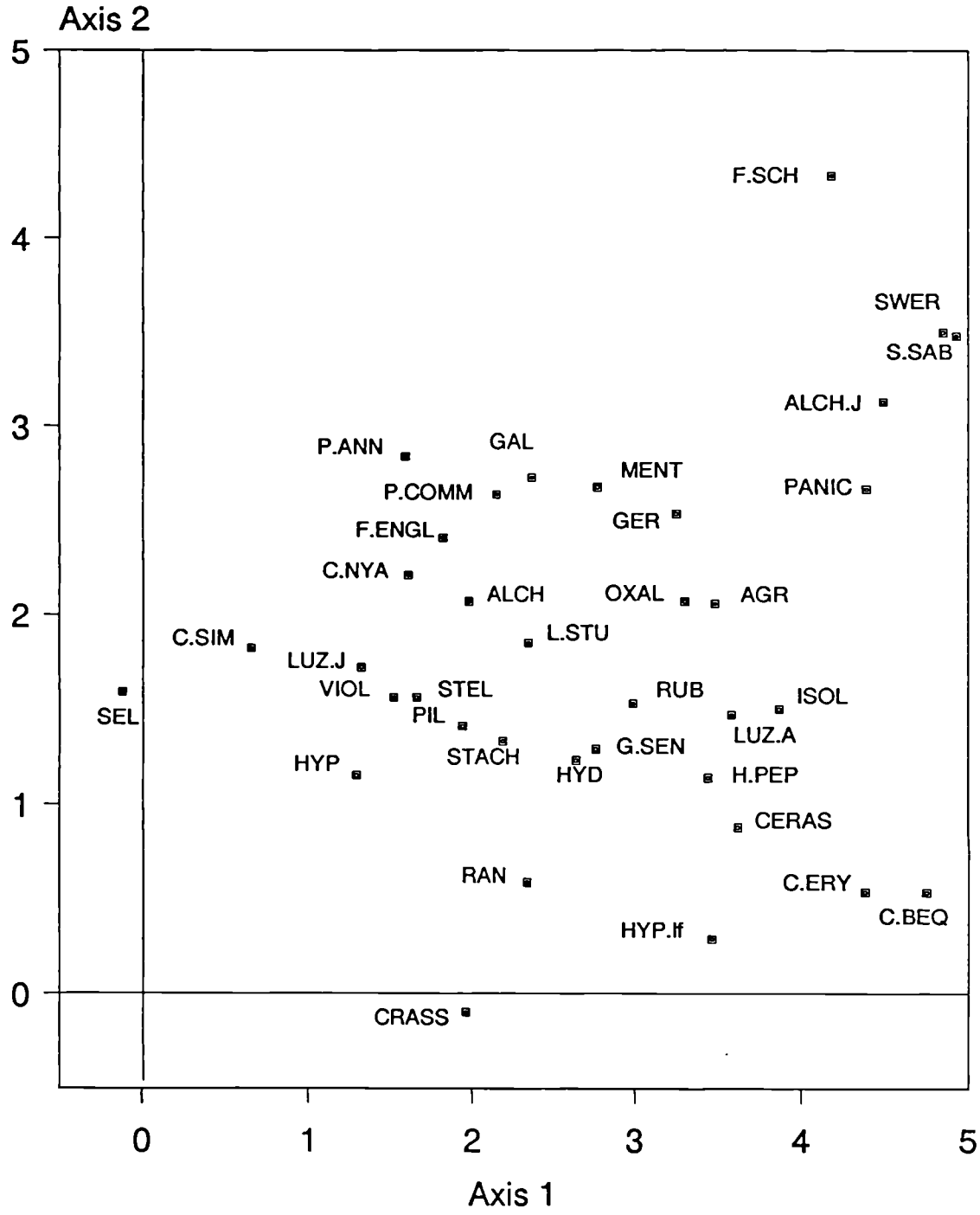


Table 2.6 Eigenvalues of each of the first two axes of the ordination plots (Figures 2.10-2.17) and the correlation coefficients between altitude, angle of slope and the ordination axes. None of the correlation coefficients were particularly high, implying that differences in the spread of plant species along one gradient cannot be solely attributed to these environmental variables.

	Axis 1			Axis 2		
	Eigen-value	Altitude	Slope	Eigen-value	Altitude	Slope
Bamboo	0.79	-0.074	0.085	0.51	0.140	-0.120
Saddle	0.67	-0.351	-0.311	0.46	0.086	0.099
Meadow	0.87	0.275	-0.092	0.49	0.046	0.149
Herbaceous	0.46	-0.462	-0.342	0.32	-0.497	-0.373
Brush Ridge	0.56	0.192	-0.079	0.32	-0.437	-0.234
Giant *Lobelia*	0.52	0.026	-0.001	0.37	-0.257	0.027
Alpine	0.64	0.010	-0.086	0.44	-0.028	-0.144
Karisimbi meadows.	0.90	0.268	-0.084	0.51	0.320	0.227

ordination axes (Jongman, Ter Braak & Van Tongeren 1987). Therefore a high eigenvalue indicates that a habitat type has a more patchy distribution of plant species because the degree of separation along the axis is higher.

2.4 Discussion

In order to understand how a herbivore lives and interacts with its environment it is important to know something about the availability of the plants upon which it feeds. Whilst this can be investigated at various levels, this study has concentrated on gross habitat distinctions and the pattern in the distribution of individual plant species. The habitats could be identified visually as being floristically distinct for at least some plant species and this was confirmed when the relative biomasses of plant species were considered between habitats (Tables 2.2 and 2.3). However, within a habitat there were also non-random distributions of plant species. The results of the DCA ordinations showed that gradient lengths longer than four standard deviations were common which meant that there were plant species that were probably never found together in the same plot. These plant separations could be partly explained in many instances by altitudinal changes or differences in the angle of slope. However altitude or slope per se does not explain why a change in either of these factors affected the distributions of the various species of plants. Factors such as temperature, water retention capacity, soil nutrient status and others will govern the presence or absence of particular plant species. This study has shown that rainfall differed little with altitude and if anything increased with altitude at certain times of year, which does not support the theory of periodic water shortage at high altitudes preventing the growth of certain plant species (Whitmore 1989). Water shortage may occur if it is frozen at certain times of year, which is possible as snow and frost occur on the summits of the volcanos. However this ice usually thaws during the day and does not occur that regularly.

When all the ordination diagrams are compared it can be seen that there are many plant species that are often found together or near each other on the plot. For example, where *Laportea alatipes* and *Galium* spp. occur in the same habitat they are nearly always found near each other in the ordination plot. In the United Kingdom a similar association between *Urtica dioica* and *Galium aparine* has been identified. Here these two species tend to be found on soil with high nitrogen and phosphorus concentrations, often where animals have defaecated or urinated (Piggott & Taylor 1964). It may be that the nettle, *Laportea*, also is an indicator of high phosphorus concentrations as *Urtica* is thought to be. Dondeyne's study (1989) of soil nutrients up the volcano Bisoke showed the soils at different altitudes to be fairly rich in nutrients. The carbon to nitrogen ratio, however, was high, implying that organic material breaks down slowly. Soil pH may drop slightly with altitude, becoming more acidic (changing from pH 6.0 to pH 4.5), but more samples are needed to confirm this.

It is possible that light levels may affect the distributions of certain plant species. Rice and Bazzaz (1989) showed that specimens of *Abutilon theophrasti* growing at uniformly low or high light intensities tended to fit a curvilinear regression of height against mass such as *Crassocephalum ducis-aprutii* (Figure 2.2). Specimens that were initially given low light intensities and then were transferred to high light intensities seem to fit the curve and line model of *Laportea alatipes* (Figure 2.2). The species that require this curve and line model are the ones that tend to be found in areas where canopy cover is higher, which might indicate that light levels are affecting certain plants in the Birungas. Therefore low light levels may also be a means whereby some plants are excluded from certain regions, thereby contributing to the patchiness of the environment.

Whittaker (1977) found that in the Himalayas plant species diversity was reduced with an increase in altitude. Therefore the increase in plant diversity with altitude in the Birungas is unexpected. This study showed that this was due to a dominance of

tall herbs at lower altitudes, although what causes this is unknown. It might be due to a greater availability of soil nutrients causing an effect similar to eutrophication, although Dondeyne (1989) did not find a great variation in soil nutrients. Another explanation might be that there is heavy disturbance to the vegetation at lower altitudes or that heavy selective feeding by herbivores promotes the growth of those plants not eaten. Both these ideas are plausible but untested.

Whilst the causes of the pattern in the distribution of plant species are at present unknown, the actual presence of pattern indicates that the environment is not uniform. This shows that there will be a greater number of available niches for animal species, which will allow a greater separation between potential competitors such as the herbivores in this study. In fact the total biomass per square metre of plant material found in this study was similar to that found in the Serengeti (McNaughton 1979) where the animals had been excluded. This high plant biomass, coupled with the fact that there are a wide variety of niches available implies that the Birungas has the potential to carry a high biomass of herbivores and this is the topic of the following chapter.

CHAPTER 3

THE SPATIAL DISTRIBUTION OF HERBIVORE BIOMASS IN THE BIRUNGAS.

3.1 Introduction.

Given the variability shown in Chapter 2 that existed between habitats in the Birungas in terms of plant species composition, it was necessary to investigate how the five herbivores were distributed in relation to this variation. Leuthold (1978), in Tsavo National Park, showed that among different species of browsing ungulates there was a fair degree of separation between them despite their similar diets because they used the habitat differently. De Boer & Prins (1990) also showed that for herbivores in Lake Manyara National Park a low overlap in habitat usage was associated with interspecific competition for food. A high overlap was found for those species which had a symbiotic effect upon their food supply, although this could occur where neither species affected each other.

In order to investigate the degree of overlap between species in their use of the available habitats it is necessary to census each species in each vegetation type. Censusing animals can be done in various ways depending upon visibility. In the savannas of East and South Africa most censusing is done from aircraft. Transects are flown over the region and animals counted directly or photographed and counted from the prints (Norton-Griffiths 1973, Sinclair 1972, 1977, Sinclair & Norton-Griffiths 1979). This technique only works for large species that are highly visible. Small antelope that can hide in clumps of trees or bushes cannot be counted accurately this way. Direct counts can also be done by walking or driving along transects (Eberhardt 1978, Burnham, Anderson & Laake 1980). These techniques assume that the animals

do not move before they are seen and that the visibility of the animals is constant over each transect. In order to obtain reasonable estimates of the population, visibility must be good over a fair distance, otherwise few animals are seen and the standard errors are consequently large.

A technique common in rodent censusing is the "capture-mark-recapture" method (Martin & Dickinson 1985). This technique has also been applied to larger animals such as kangaroos (Southwell 1989) but is highly labour intensive and can be stressful for the animals. For forested habitats drive techniques may be used, counting the animals as they are driven past observers. However, I have been involved in deer-catching operations where even the third or fourth drive through a completely enclosed area produced further animals that had been missed. This technique is also highly labour intensive and in the case of the larger species, such as buffalo and elephant, it could be dangerous. Therefore in this study, as in most counts of animals in forests, it was decided to use indirect assessments of animal presence, the most common technique being the counting of dung (Neff 1968, Wing & Buss 1971, Jachmann & Bell 1979, 1984, Koster & Hart 1988).

Two techniques can be used: *clearance plots and standing crop counts (Staines &* Ratcliffe 1987). The clearance plot method involves clearing many marked plots and then counting and removing faecal droppings at regular time intervals. As long as the interval between counts is shorter than the time it takes for a dropping to decay completely, then these counts can be used to estimate animal numbers. In order to estimate animal numbers using this technique, an estimate of the defaecation rate of the animal is required. Standing crop counts only require one visit to a site and hence allow a greater area to be censused. However, to obtain actual animal numbers, the counts obtained must be corrected for the defaecation rate and also for the rate at which droppings decay. The decay of droppings is usually assumed to be constant and logarithmic (McClanahan 1986, Barnes & Jensen 1987). The standing crop count,

when used to census animals, also assumes that a state of equilibrium exists between the number of droppings deposited daily and the number disappearing through decomposition. For the elephants, which often use different regions of the available habitat during different seasons, this may not be a valid assumption. Wing & Buss (1971) gave 80 days as the half life of elephant dung in a forested area. The same study showed that the elephants were using different areas of the forest every three months. It was therefore very unlikely that any steady state was reached in this forest, or if it did occur it was for too short a time to be able to carry out an accurate census. Despite such problems the standing crop count is worth considering in forested areas, particularly where the vegetation is dense, because the regular clearing of plots that is required for the clearance plot counts will open up the vegetation thereby promoting the use of the plots by animals. Barnes & Jensen (1987) noted that elephants preferentially used paths or cut transects and therefore any counts based on revisiting transects would give an inflated population estimate.

Counts of dung can be done within plots or strip transects, where all droppings are counted within a boundary, or alternatively all droppings seen from a transect can be counted. If this latter method is used then the distance the dropping lies from the central line of the randomly placed transect must be measured. Plotting the number of droppings seen at different distances from the midline of the transect usually gives a curve that drops off as distance increases (Burnham et al. 1980, Barnes & Jensen 1987). Then a detection function can be fitted to these data (usually a fourier estimation function fits well) to calculate the actual density of the droppings, given that there are some that are being missed by the observer (Burnham et al. 1980).

One of the advantages of dung counts is that differential use of habitats can be measured. This is less practical with visual counts because correction factors for differential visibility in different habitats must be calculated. The assumption that is made in comparing dung counts between habitats is that defaecation within a habitat is

in proportion to the animals use of that habitat. This assumption has rarely been tested and was found to be invalid for Mule deer (*Odocoileus hemionus*) (Collins & Urness 1981). However, Loft & Kie (1988) and Leopold, Krausman & Hervert (1984) argued that, in cases where it has been tested, the ranking of pellet distributions is the same as those of the habitat use even if the actual number of deer do not fit the observed proportional use of the habitats.

There is a lot of scope for error in the use of dung counts to estimate the size of animal populations and their use of the available habitats. In certain habitats, however, it is still the most effective technique for providing this kind of data and consequently will continue to be used. So long as its limitations are recognised and care is taken to ensure accurate counts and correction factors, it will remain a valuable technique.

3.2 Methodology

3.2.1 Standing crop counts

Habitat use by each of the five herbivores was studied during the four seasons of the year (see Chapter 2). A baseline was drawn on a map of the study area running east-west through Karisoke, and divided into seven equally spaced sections. Within each section a point was chosen randomly using random number tables and compass bearings taken from this point to the major landmarks in its vicinity. From these the point could be found on the ground (if the point was in the middle of the forest a line was run north to a major path where it was easier to locate). Transects were then cut north and south and this whole process was repeated each season. The transects walked were strip transects, three metres wide and up to 2km in length and were searched continuously for buffalo, elephant and gorilla droppings. Bushbuck and duiker pellet groups were searched for separately at 20 pace intervals in 5x2 metre plots by two observers as this dung was easily missed over the whole transect. A pellet

group/dropping was counted if at least half of it was within the plot or transect. Elephant or buffalo dung which was more than half covered with vegetation growing through the dung was deemed to have fully decomposed. Pellet groups were fully decomposed when pellet shape was unrecognisable and if there were less than 30 pellets per group. In distinguishing bushbuck and duiker pellets, shape of pellet and pellet group, internal texture and occasionally odour were all used as identifying features.

For each species dung was assigned to one of three categories: fresh, dry and old. At each antelope plot and whenever elephant, buffalo or gorilla dung was found, the habitat type, altitude and the two main vegetation types (eg. clover, nettle) were noted. In the case of the three largest herbivores, the distance from the midline of the transect to the dropping was measured to the nearest ten centimetres to check that all droppings were being found across the transect. At least 200 antelope plots were searched in each habitat type; this sometimes required extra transects (all randomly located) where the area of habitat was small compared to the study area. The length of the transects was determined by counting paces, each pace being 70 centimetres long and checked at regular intervals by the use of a marked walking stick.

3.2.2 Defaecation rates

Defaecation rates for the elephant and buffalo were determined in the following manner. A small herd of about five to ten animals would be found and the time noted. The following day their trails would be followed counting all fresh droppings along it until the group was found again. It was important to check that the number of animals was the same from one day to the next and several counts were discarded because this was not possible. Similarly, if the trail was lost in a large meadow then the count would be abandoned because there was the possibility of missing some animals if the herd fanned out. Bushbuck were observed from trees for one minute periods separated

by breaks of one minute. Scans of all visible antelope were also taken every two minutes to record their behaviour. If an animal started to defaecate during the one minute period it was recorded. The site was noted and later visited to check that there had been a defaecation and that greater than 30 pellets had been produced (fewer pellets were not counted). The figure of 30 pellets was chosen for both the transect counts and the defaecation rate because most pellet groups were larger than this. Small groups were not counted because they would decompose more quickly. It was not possible to measure the defaecation rate at night for the bushbuck,although they were active both day and night,so that it was assumed that it was the same. Initially similar data were collected for duiker but it was soon found that these animals seemed to defaecate more frequently along territorial boundaries around the Karisoke research centre. Territory boundary was determined from interactions between males, which varied from chases to head butting (similar to goat fights). As this was the case, the choice of observation site could have affected the estimate of the defaecation rate. Therefore a rate was taken from the literature for a bay duiker (*Cephalophus dorsalis*) which was fed foliage rather than fruit at the time of the trial. This species is a similar mass to the Black-fronted duiker and showed a similar defaecation rate to other duiker species (Koster & Hart 1988).

3.2.3 Gorilla counts in each habitat

Gorilla dung was scarce even when counted over the whole transect and therefore habitat use in this species was studied in a different manner. For most of the time the only gorilla groups in the study area were the research groups and these were followed daily by Rwandan trackers. There was one group of four wild animals (the Amahoro group) which occasionally entered the study area but this was probably very rare as signs were only found a couple of times along the transects. Gorilla researchers were asked to note which habitat the dominant silverback was in at 11.00 am each time the group was visited. This time was chosen because it was a period when the gorillas

were feeding or resting between feeding bouts and the habitat where these animals feed was of more interest than where they spent the night. The number of days each group spent in the study area was obtained from the trackers daily reports. Having found that gorilla dung was scarce no attempt was made to study the defaecation rate or decomposition rate of the dung.

3.2.4 Decomposition rates of dung

The decomposition rate of dung was studied as follows. Twenty bushbuck pellet groups were placed in each habitat type each month and visited at weekly intervals to record how many had disappeared. A group was recorded as "gone" when either the pellets were unrecognisable or there were fewer than thirty pellets to conform to criteria used on the transects. Fresh duiker dung was more difficult to find and therefore only 20 pellet groups were placed in the Saddle zone. The rates of decay of these droppings were related to the bushbuck decay in the same habitat and then extrapolated to other habitats using the bushbuck data. Buffalo pats were marked or placed in five of the habitat types; Bamboo, Saddle, Meadow, Herbaceous and Karisimbi meadows. The habitats high on Bisoke were little used so that, except for one period when a herd left several pats on the summit, the rates were not measured here. Elephant dung was marked in the Bamboo, Saddle and Herbaceous habitats as these were the only habitats visited by this species..

3.2.5 Clearance plot counts

In order to provide a comparison with the above census technique a clearance plot count was done during the main wet and dry seasons in 1989. In each habitat type twenty plots (10x5 metres) were marked out, visited and cleared of dung at roughly monthly intervals during March to September. Due to the difficulty of finding randomly placed plots in the dense vegetation it was decided to place them near paths

that were used for other aspects of this study. Data on the vegetation types within each of the habitats (section 3.2.1) were used to determine where these clearance plots were placed. For each habitat, the twenty $50m^2$ plots were placed in a similar ratio of vegetation types to that found on the transects. For example, 50% of the antelope plots searched on the transects contained clover or grass in the Saddle zone and therefore ten of the clearance plots also had grass and clover. On the initial clearance of the plots the dung of each species was counted. This count was then compared with the most recent transect count in the same habitat to obtain a correction factor by which the non-random placing of the plots could be corrected.

3.3 Results

3.3.1 Defaecation rates

Defaecation rates used in this study for the four ungulates are given in Table 3.1. It was only possible to follow the elephant herd twice while it was in the study area; which gave an estimate of 16.2 defaecations d^{-1}. This figure is similar to the 17 d^{-1} given by Wing & Buss (1970) for a elephants in a forest in Uganda and therefore this figure of 17 d^{-1} was used in this study. Prins & Reitsma (1989) gave a figure for buffalo of 10 pats d^{-1}, which is similar to that found in cattle (H.H.T. Prins pers. comm.). In the present study a value of 5.1 d^{-1} was obtained from fifteen days and nights of tracking and amounts to 3067 buffalo hours. The standard error of this estimate is 0.27 and none of the estimates exceeded 7 pats d^{-1}. Many other periods of tracking were attempted but not included with these data because I could not be certain that all the buffalo trails had been followed or that the small herd had stayed intact. It is possible some droppings may have been missed but in order to obtain a value of 10 defaecations per day this would mean that the Rwandan tracker and I both missed a mean value of 43 droppings over each of the 15 counts which is not possible. Therefore I used my estimate of 5.1 pats d^{-1}.

Table 3.1 Defaecation rates used in the correction of dropping density to actual animal numbers. The rates for the duiker and elephant were obtained from the literature. Two measures of the elephant defaecation rate were obtained by following one herd and the mean rate obtained is not dissimilar to that used from the literature.

	Number per day	
Buffalo	**5.1**	(3067 buffalo hours)
Bushbuck	**19.0**	(25.2 hours observation)
Duiker	**4.4**	(Koster & Hart 1988)
Elephant	**17.0**	(Wing & Buss 1971)
(16.2 obtained from two measures)		

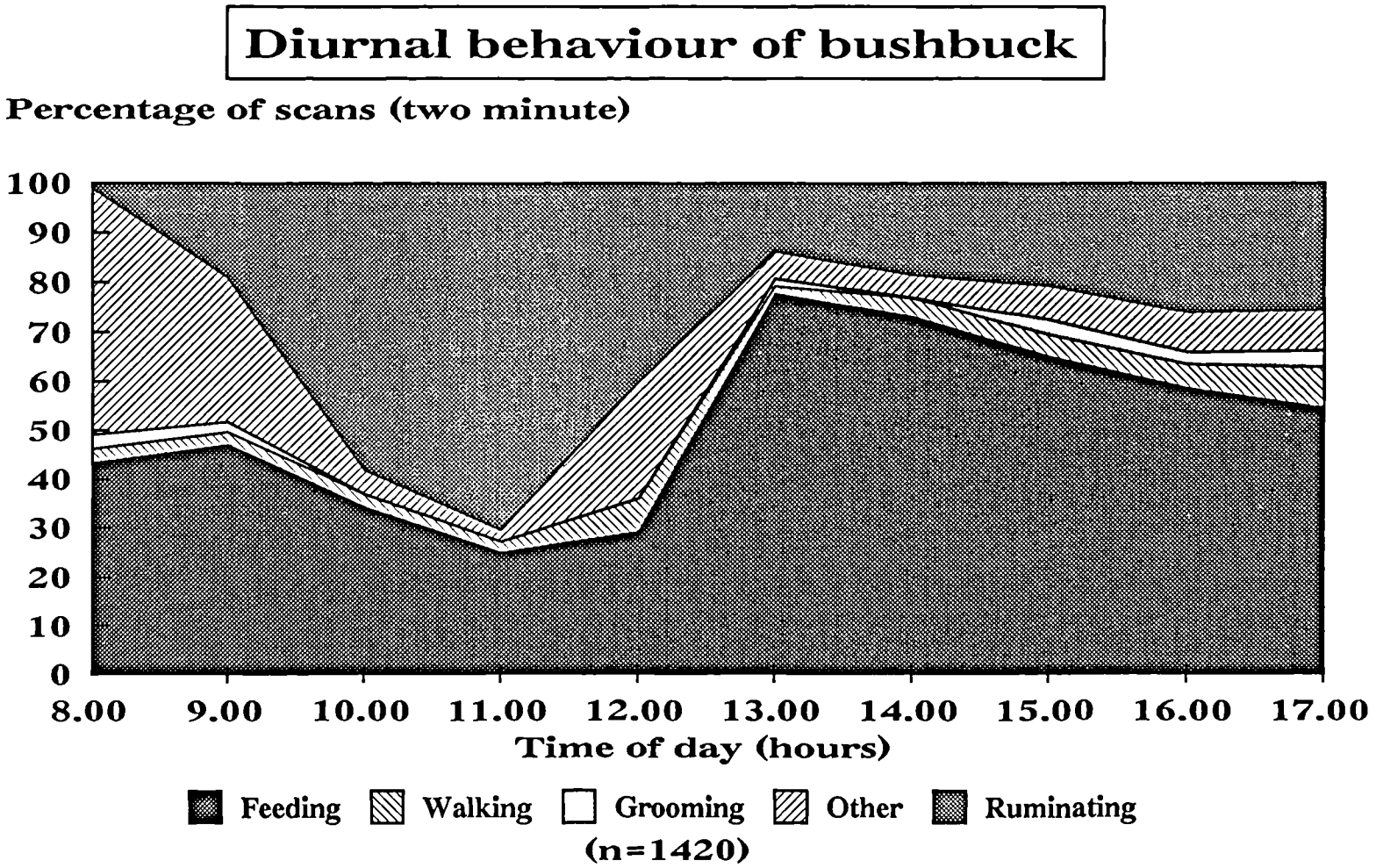


Figure 3.1 Diurnal behaviour of the bushbuck. The percentage of two minute scan samples of different behavioural activities for different hourly periods between 0800 hours and 1700 hours. There are significant differences in feeding, ruminating and other activities at different times of the day (see text).

The diurnal behaviour of the bushbuck is summarised in Figure 3.1. There is an obvious switch in behaviour from ruminating in the late morning to feeding in the afternoon. There was no significant difference in walking and grooming throughout the day (X^2=11.7 - walking, X^2=12.6 - grooming). However the other three behaviour patterns were significantly different at different times of the day (feeding: X^2=158.5, d.f.=8, P<0.001; ruminating: X^2=149.8, d.f.=8, P<0.001; other: X^2=181.5, d.f.=8, P<0.001). A test of variation in the defaecation rate throughout the day however was not significant (X^2=2.76, d.f.=2, P>0.05). Therefore the behaviour of the bushbuck does not appear to affect the rate of defaecation.

3.3.2 Clearance plot density estimates

Table 3.2 shows the densities of three of the ungulates from the clearance plot counts. Friedmans ANOVA of the counts from March to May against counts from June to August were all non-significant for each habitat and species. Therefore there was no detectable difference in their use of the of the study area between wet and dry seasons. Table 3.3 shows the actual numbers of animals within each habitat, calculated by multiplying the density (Table 3.2) by the area of each habitat (Table 2.1), and gives the mean density for the whole study area.

3.3.3 Standing crop density estimates

Analysis of the dropping decomposition rates showed that at certain times of year the dung decayed in a logarithmic manner but at other times the decay was more sigmoidal (Figure 3.2). The sigmoid curves tended to come from dung deposited in the dry season which was dried by the sun and could in some cases last through the subsequent wet season. Harestad & Bunnell (1987) found that moisture was one of the major environmental factors which affects dung decay of Black-tailed deer in Canada and this, coupled with the degree of exposure to the sun, seemed to be the case in the

Table 3.2 Herbivore densities (No. Km^{-2}) calculated from clearance plots. The standard errors are shown in parentheses.

Habitat type.	Bushbuck	Duiker	Buffalo
Bamboo	**31.3** (±4.8)	**4.7** (±0.8)	**7.2** (±4.2)
Saddle	**59.9** (±2.4)	**16.0** (±2.0)	**2.8** (±1.2)
Meadow	**16.6** (±2.6)	**13.1** (±3.2)	**16.3** (±2.5)
Herbaceous	**63.6** (±3.6)	**6.6** (±2.5)	
Brush Ridge	**43.1** (±4.4)	**21.6** (±4.3)	
Giant *Lobelia*	**34.1** (±2.4)	**11.0** (±2.7)	
Alpine	**13.7** (±3.7)	**7.1** (±3.4)	**0.4** (±0.4)
Karisimbi meadows	**31.4** (±4.18)	**21.1** (±3.6)	**22.5** (±3.9)

Table 3.3 The total number of herbivores in each habitat based upon clearance plot counts of dung. Numbers were calculated using the densities given in Table 3.2 and the area of each habitat type (Chapter 2). The total number of each herbivore species in the study area was then used to calculate a mean density for this region. Standard errors are shown in parentheses.

Habitat type.	Bushbuck	Duiker	Buffalo
Bamboo	**8.9** (±1.4)	**1.3** (±0.2)	**2.1** (±1.2)
Saddle	**385.0** (±15.4)	**103.0** (±12.9)	**18.0** (±7.7)
Meadow	**4.9** (±0.8)	**3.8** (±0.9)	**4.8** (±0.7)
Herbaceous	**138.3** (±7.8)	**14.4** (±5.4)	
Brush Ridge	**41.6** (±4.2)	**20.8** (±4.1)	
Giant *Lobelia*	**22.0** (±1.6)	**7.1** (±1.7)	
Alpine	**9.4** (±2.5)	**4.9** (±2.3)	**0.3** (±0.3)
Karisimbi meadows	**21.8** (±2.9)	**14.7** (±2.5)	**15.7** (±2.7)
Total	**631.9**	**170.0**	**40.9**
Density in study area. (no.km^{-2})	**51.9**	**14.0**	**3.4**

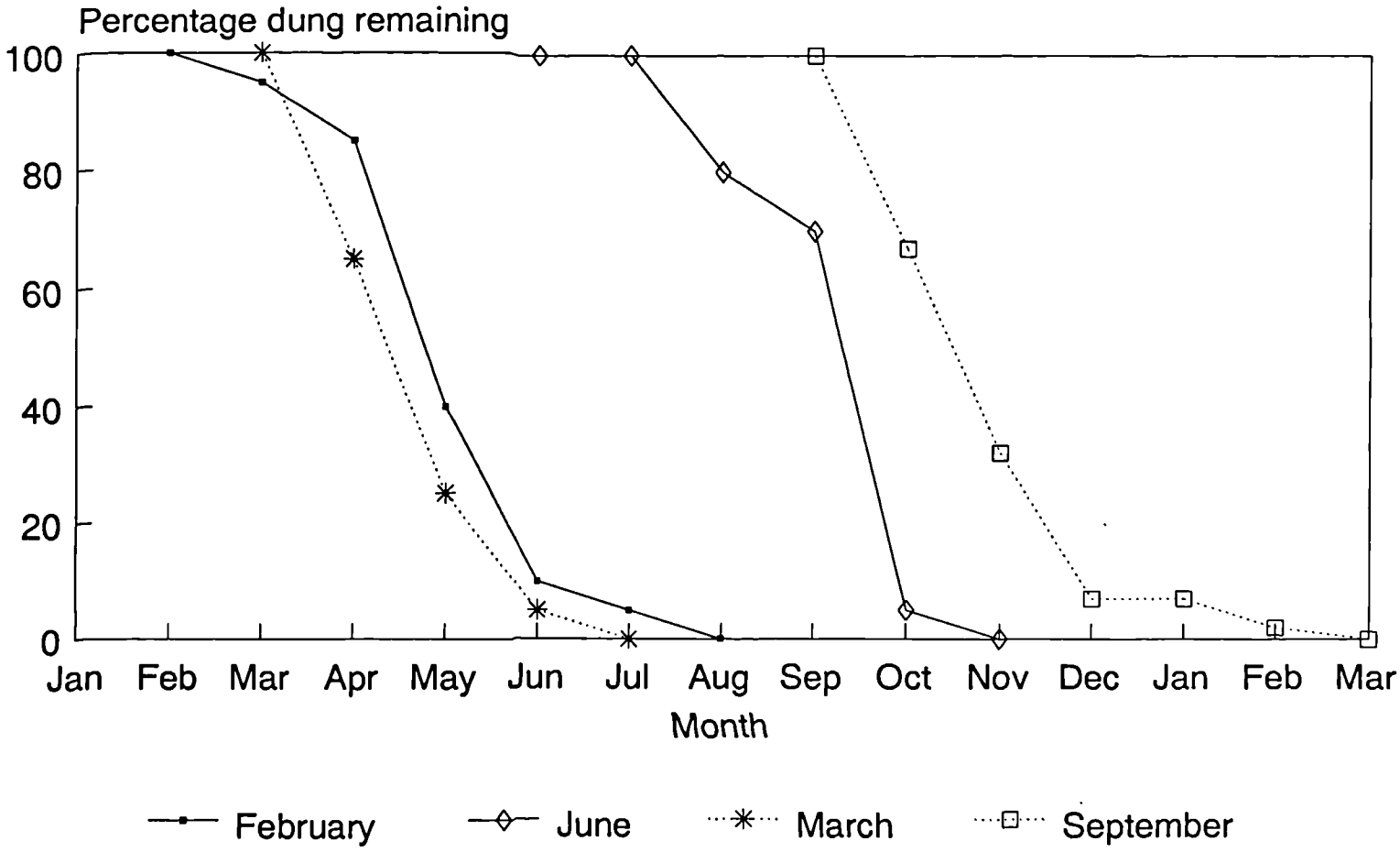


Figure 3.2 The decay of 20 bushbuck pellet groups at different times of the year. This graph shows the decay in the Herbaceous zone for selected months and shows that the pellets deposited in drier months tend to have a sigmoidal decay rather than exponential.

Birungas. It was also obvious that dung decay over the three month period of a season was not constant. Therefore the assumptions that are made for standing crop counts were being violated on at least two accounts (see section 3.1) and it was decided to model the decay of droppings.

The model is summarised in Figure 3.3. Buffalo dung was monitored seasonally because of the long time required to break down but bushbuck and duiker dung had to be monitored for each month. This figure shows the model for the buffalo with the four seasons because it is easier to visualise than a 12x12 matrix which had to be constructed for the bushbuck and duiker. For each season dung decay was entered as the percentage remaining from previous seasons. Each column of the matrix shows that for a particular season, 100% of dung was present for that season's depositions and then the other percentages were what remained from previous seasons (see row title for the period in question). An initial estimate of dung deposited in each month "E" was than made and fed through this matrix to give the amount of dung expected in each cell of the matrix. Each column for the amount of dung expected was then summed to give an estimate of the amount of dung that should be found using a transect count. The actual count during each season was then divided by this expected count and the ratio obtained was multiplied by "E" to give a new value for "E". This new value was then fed back through the matrix and the process continued iteratively. Whatever the starting values were for "E" this process approached the actual count until there was no difference at which point "E" was read to obtain the amount of dung deposited during a particular season. The main assumption this model makes is that the number of animals present during one season of one year is the same as the same season the following year. For the region around Karisoke this was a valid assumption because of the protection this area had received. Tables 3.4 to 3.7 give the density of bushbuck and buffalo obtained by this method and the estimated numbers of animals in each habitat type. Buffalo dung distribution away from the midline of the transect was tested to see if there was a significant drop in visibility using X^2 tests; for each

Figure 3.3 The model used to obtain the amount of dung deposited each day by a herbivore species. This uses the measure of the percentage of dung that remains in each season obtained from the decomposition trials.

Dung deposited per day (input an estimate - "E")	**100**	**50**	**50**	**50**
	▼	▼	▼	▼
Percentage dung remaining:	**Dec-Feb.**	**Mar.-May**	**June-Aug.**	**Sep.-Nov.**
Dec-Feb.	100%	25%	20%	0%
Mar-May.	0%	100%	40%	5%
Jun-Aug.	15%	0%	100%	60%
Sep-Nov.	50%	5%	0%	100%

Dung contribution from each season: (for Mar-May)	25 50 0 2.5	Percentages multiplied by dung input.
Expected total:	77.5	
Actual transect count:	100	
Correction factor:	(100/77.5) = 1.29	

For next run input: 50x1.29 = 64.5 as the new quantity of dung deposited during the period of Mar-May. The quantities for each season will vary from now on because of the different percentages in each column. To obtain the dung contribution for each season, the percentages for each row are multiplied by the dung input for that season (ie. 100x25% = 25, 50x100% = 50, 50x5% = 2.5).

Table 3.4 Bushbuck density (No.Km^{-2}) in each habitat type obtained from the transect (standing crop) counts and given for each season. Standard errors are given in parentheses.

Vegetation type.	Dec.-Feb.	Mar.-May	Jun.-Aug.	Sep.-Nov.
Bamboo	**28.7** (±3.6)	**24.0** (±4.6)	**43.2** (±5.1)	**21.4** (±3.5)
Saddle	**43.8** (±3.0)	**40.9** (±1.9)	**53.6** (±3.3)	**38.7** (±1.7)
Meadow	**17.8** (±1.7)	**28.1** (±6.4)	**19.8** (±2.1)	**12.6** (±3.8)
Herbaceous	**25.1** (±2.9)	**48.4** (±4.8)	**25.8** (±2.1)	**27.7** (±2.8)
Brush Ridge	**17.5** (±3.1)	**27.7** (±2.9)	**25.3** (±3.5)	**13.3** (±2.1)
Giant *Lobelia*	**15.4** (±2.7)	**31.7** (±3.6)	**19.4** (±2.7)	**16.1** (±2.4)
Alpine	**11.5** (±1.6)	**13.6** (±2.3)	**8.0** (±1.2)	**11.2** (±2.4)
Karisimbi meadow	**15.4** (±1.8)	**27.3** (±4.4)	**20.2** (±2.6)	**22.2** (±3.4)

Table 3.5 Bushbuck numbers calculated for each habitat type and season using the density estimates in Table 3.4 and the area of each habitat type determined in Chapter 2. The mean density of bushbuck in the study area was calculated from the total number of animals. Standard errors are given in parentheses.

Vegetation type.	Dec.-Feb.	Mar.-May	Jun.-Aug.	Sep.-Nov.
Bamboo	8.2 (±1.0)	6.8 (±1.3)	12.3 (±1.5)	6.1 (±1.0)
Saddle	281.6 (±19.3)	262.7 (±12.1)	344.2 (±21.3)	248.4 (±10.8)
Meadow	5.2 (±0.5)	8.2 (±1.9)	5.8 (±0.6)	3.7 (±1.1)
Herbaceous	54.5 (±6.2)	105.3 (±10.4)	56.1 (±4.6)	60.2 (±6.1)
Brush Ridge	16.9 (±3.0)	26.7 (±2.8)	24.3 (±3.4)	12.8 (±2.0)
Giant *Lobelia*	10.0 (±1.7)	20.5 (±2.3)	12.6 (±1.7)	10.4 (±1.6)
Alpine	7.8 (±1.1)	9.3 (±1.6)	5.5 (±0.8)	7.6 (±1.7)
Karisimbi meadow	10.7 (±1.3)	19.0 (±3.1)	14.0 (±1.8)	15.4 (±2.3)
Total	394.9	458.5	474.8	364.6
Mean density in study area. (No.km^{-2})	32.4	37.7	39.0	30.0

Table 3.6 Buffalo densities (No. Km^{-2}) in each of the eight habitat types obtained from the transect (standing crop) counts. Densities are given for each season of the year. Standard errors are given in parentheses.

Habitat type.	Dec.-Feb.	Mar.-May	Jun.-Aug.	Sep.-Nov.
Bamboo	**0**	**10.5** (±0.9)	**0**	**9.5** (±1.6)
Saddle	**2.0** (±0.3)	**4.2** (±0.4)	**2.3** (±0.3)	**3.2** (±0.2)
Meadow	**15.7** (±0.8)	**8.4** (±0.3)	**12.2** (±0.4)	**10.7** (±0.5)
Herbaceous	**0.9** (±0.3)	**0.7** (±0.1)	**2.0** (±0.2)	**2.2** (±0.3)
Alpine	**0**	**1.6** (±0.8)	**1.1** (±0.1)	**0.5** (±0.1)
Karisimbi meadows	**8.1** (±0.9)	**14.3** (±0.9)	**11.9** (±0.7)	**4.0** (±0.6)

Table 3.7 Buffalo numbers in each habitat type throughout the year. Numbers were calculated using the densities given in Table 3.6 and the areas of the vegetation types given in Chapter 2. Mean densities of the buffalo over the whole study area were calculated from the total number of animals. Standard errors are given in parentheses.

Habitat type.	Dec.-Feb.	Mar.-May	Jun.-Aug.	Sep.-Nov.
Bamboo	0	3.0 (±0.3)	0	2.7 (±0.5)
Saddle	12.7 (±1.9)	27.1 (±2.6)	15.1 (±1.9)	20.5 (±1.3)
Meadow	4.6 (±0.2)	2.5 (±0.1)	3.6 (±0.1)	3.1 (±0.1)
Herbaceous	1.8 (±0.7)	1.5 (±0.2)	4.3 (±0.4)	4.8 (±0.7)
Alpine	0	1.1 (±0.5)	0.7 (±0.1)	0.3 (±0.1)
Karisimbi meadows	5.6 (±0.6)	10.0 (±0.6)	8.3 (±0.5)	2.8 (±0.4)
Total	24.7	45.2	32.0	34.2
Mean density in study area. ($No.km^{-2}$)	2.0	3.7	2.7	2.8

habitat there was no significant change. This meant that it was possible to use the transect counts without having to correct for missed droppings. Duiker dung decayed very quickly in the wet season and, unlike the other dung, was strongly affected by the weather conditions on the day it was deposited so that this technique could not be used to census these animals.

Table 3.5 shows that the total bushbuck population varied between seasons. The bulk of the variation came from the Saddle and Herbaceous habitat types because these are the largest habitats in surface area. The standard errors of the counts give one measure of the accuracy of the animal densities, although this does not include possible errors in the dung decomposition rates. Therefore in order to test differences between seasonal use of the Saddle and Herbaceous habitats a sensitivity analysis was performed on the model. Dung decomposition was varied by +/- 10% for each season in the model and a t-test performed on all the possible combinations of this variation for the four seasons to see if there was a difference between seasons. For the Saddle zone there was a significant increase in bushbuck numbers during June-August over all other seasons ($P<0.001$ for all three tests). For the Herbaceous zone, March to May was significantly different at the $P<0.001$ level to the other three seasons. None of the other seasons differed significantly between each other for either habitat. Sensitivity analysis on the buffalo data showed that for the two types of meadow there was a significant difference in use between all seasons at the $P<0.05$ level and most tests were significant at the $P<0.001$ level.

Transect counts of dung in the Saddle zone were large enough to divide this habitat into two: west and east or north and south. Use of the north versus the south of this habitat and east versus the west by the bushbuck are shown in Table 3.8. During June to August there appears to be an increase in bushbuck numbers in the western half of the Saddle and sensitivity analysis showed that this was significantly different to the count obtained in March to May. Table 3.9 shows the division of the Saddle zone into

Table 3.8 The density of bushbuck (No. Km^{-2}) in different regions of the Saddle zone based on the transect counts of dung. Densities are given for the North or South of this habitat and the East or West. Standard errors are given in parentheses.

Region of Saddle.	Dec.-Feb.	Mar.-May	Jun.-Aug.	Sep.-Nov.
North	49.5 (±4.6)	45.8 (±2.8)	68.9 (±5.3)	48.7 (±2.5)
South	37.9 (±3.8)	36.6 (±2.6)	38.9 (±3.8)	29.6 (±2.3)
West	42.2 (±8.5)	32.5 (±1.3)	56.2 (±8.3)	44.3 (±1.7)
East	39.8 (±3.3)	56.6 (±4.0)	54.6 (±7.7)	34.4 (±2.8)

Table 3.9 The density of buffalo (No. Km^{-2}) in different regions of the Saddle zone based on the transect counts of dung. Densities are given for the North or South of this habitat and the East or West. Standard errors are given in parentheses.

Region of Saddle.	Dec.-Feb.	Mar.-May	Jun.-Aug.	Sep.-Nov.
North	**3.3** (±1.0)	**5.5** (±1.7)	**3.0** (±1.0)	**3.3** (±1.2)
South	**0.75** (±0.5)	**3.1** (±1.2)	**1.7** (±0.8)	**3.1** (±1.1)
West	**0.6** (±0.5)	**7.3** (±1.9)	**1.2** (±0.8)	**5.4** (±1.6)
East	**3.0** (±1.0)	**1.3** (±0.8)	**3.5** (±1.1)	**1.3** (±0.7)

the same four regions for the buffalo data. During the wet seasons the buffalo used the western half of the study area and during the dry seasons they used the eastern half.

Elephant densities were calculated from the actual number of animals and the time they spent in the study area (Table 3.10). A group of seven animals (four adults and three juveniles) spent 108 days in the study area during the June-August dry season in 1988. The relative dung densities could therefore be used to investigate habitat use. The distribution of dung away from the midline of the transect was tested using X^2 analysis to see if some dung was being missed, but for all habitats there was no significant difference. A steady state between dung deposition and decay was not reached in this study because dung deposited at the beginning of June when the elephants arrived, survived until the elephants had left in September. This led to possibilities of bias in the relative habitat use from dung counts, because the time at which a transect was cut and searched would have influenced the amount of dung found if dung density was continually increasing. A count done in September to November after the elephants had left, however, gave similar densities. This group was the only herd to visit the area in the two years of the study which was about 15% of the total time. Therefore an estimate of the density of elephant over the whole study period could be calculated (Table 3.10).

3.3.4 Gorilla habitat use

Gorilla habitat use is given for each of the three habituated groups in Table 3.11, combining the two wet and dry seasons together, and Table 3.12 shows the seasonal use of the habitats. Group 5 used the Bamboo seasonally, visiting it mostly during the wet seasons when the bamboo was producing shoots. They consequently spent less time in the Herbaceous zone during this time. Peanut's group use of the Alpine zone in the wet season was an anomaly because the silverback was ill during March-May 1989 and consequently did not move much. These animals were also visited by

Table 3.10 Elephant densities obtained from the transect counts in the June-August dry season in 1988. The density is also given for the elephant over the two year period of study. (Elephants spent 108 days in study area = 15% of total time)

Habitat type	Density (No.km^{-2}) (June-August)	Density for total study (No.km^{-2})
Bamboo	1.46	0.22
Saddle	0.83	0.12
Meadow	0.28	0.04
Herbaceous	0.55	0.08
Total study area	0.58	0.08

Table 3.11 The percentage number of observations of each research gorilla group in each habitat type during the wet and dry seasons. These observations include observations outside the study area aswell as within it.

Group	Bamboo	Saddle	Herbaceous	Brush Ridge	Giant *Lobelia*	Alpine
Beetsme						
Wet		54.5	19.9	16.0	4.5	5.1
Dry		52.6	23.2	17.9	2.7	3.6
Total		53.7	21.3	16.8	3.7	4.5
Group 5						
Wet	21.8	27.7	48.0	0.5	1.0	1.0
Dry	2.2	25.2	66.2	0.7		5.7
Total	13.8	26.7	55.4	0.6	0.6	2.9
Peanuts						
Wet		65.7	7.1			27.2
Dry		76.9	7.2	1.4	2.9	11.6
Total		70.3	7.1	0.6	1.2	20.8

Table 3.12 The results of Chi^2 analyses on the differential use of the habitats by each gorilla group between the wet and dry seasons (this included habitat use measured outside the study area). The results of a weighted test for all three groups combined are also given, weighting the groups evenly to correct for the differing number of observations.
(ns. = Not significant, * = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$)

	Bamboo	Saddle	Herbaceous	Brush Ridge	Giant *Lobelia*	Alpine
Beetsme (n=268)		ns.	ns.	ns.	ns.	ns.
Group 5 (n=341)	***	ns.	**	ns.	ns.	*
Peanuts (n=168)		ns.	ns.	ns.	ns.	*
Weighted Total. (n=777)	***	ns.	*	ns.	ns.	ns.

Table 3.13 The percentage number of observations of each research gorilla group within the study area, and the calculated number of animals and density throughout the study area. These measures were taken from the same census periods as the other herbivores. (Group sizes: Beetsme=12, Group 5=26, Peanuts=6)

Group	Dec.-Feb.	Mar.-May	Jun.-Aug.	Sep.-Nov.
Beetsme	55.6%	28.3%	26.1%	28.6%
Group 5	16.7%	31.5%	30.4%	36.3%
Peanuts	68.9%	0%	1.1%	11.0%
Total number of gorillas	15.2	11.6	11.1	13.5
Density in study area ($No.km^{-2}$)	1.2	1.0	0.9	1.1

Table 3.14 The percentage use by the three gorilla groups of the habitats within the study area during 1988 and 1989. The time each group spends in the study area is used to weight these figures (n=273). Habitat use is calculated for the wet and dry seasons and the results of a Chi^2 analysis is given to show where there are significant differences in the use of each habitat between seasons. (ns. = Not significant, *** = $P<0.001$).

	Bamboo	Saddle	Herbaceous	Brush Ridge	Giant *Lobelia*	Alpine
	n=25	n=62	n=90	n=36	n=14	n=16
Wet seasons	15.1	30.0	29.5	13.5	6.5	5.4
Dry seasons	0.7	23.4	39.9	20.5	7.2	8.3
Total	7.7	27.0	34.4	17.0	6.9	7.0
X^2	***	ns.	ns.	ns.	ns.	ns.

researchers more frequently than usual at this time which inflated the results. The percentage use of the study area was calculated (Table 3.13) for each group and used to weight the use of each habitat type within the study area (Table 3.14). A test of differential use of habitat between seasons by all gorillas in the study area showed that only the Bamboo is used seasonally in the study region. This is because Group 5 which contains more than half the gorillas in this area uses the bamboo during the wet seasons.

3.3.5 Vegetation use within each habitat

Use of the habitats by each of the species was also studied on a finer scale within each habitat. The dominating vegetation types (e.g. clover, grass) allocated to each plot in Chapter 2, during the botanical survey, were compared with the actual biomasses of plants to see what proportion of visual classifications fitted the actual dominant vegetation types. This is summarised in Tables 3.15 and 3.16. On average 8-9% of plots had one vegetation class misclassified (i.e. there was another plant type that contributed more to the total mass than the one classified visually) but in only 0.4% did I fail to identify both of the two dominant vegetation types. Therefore the vegetation types associated with the dung were the two most dominant in terms of biomass for at least 90% of cases. X^2 tests were used to test the difference between observed dung counts in a vegetation type and that expected given the number of antelope plots with that vegetation type present. These results are summarised for duiker, bushbuck and buffalo in Tables 3.17-3.19. Elephant and gorilla dung counts were low so that few significant differences were found. Elephant avoided bamboo stems in the Bamboo zone ($P<0.001$) but preferentially visited nettles in this habitat type ($P<0.001$). Gorillas only preferred *Senecio mariettae* in the Brush ridge zone ($P<0.001$). This is because they make their night nests in this vegetation and they usually defaecate within the nest. On this fine scale, the dung count may only show a preference for where dung is deposited and may not necessarily reflect habitat use by

Table 3.15 The misidentification of vegetation types forming the dominant biomass of measured plots. During the vegetation survey (Chapter 2) plots were assigned two vegetation types which appeared to be the most dominant before the plot was cut, dried and weighed. This table shows the percentage of plots for each habitat where at least one assigned vegetation type was not dominant in terms of biomass.

Habitat	Total plot number	Leaf mass		Total mass	
Bamboo	204	3	(1.5%)	2	(1.05%)
Saddle	554	79	(14.3%)	71	(12.8%)
Meadow	200	11	(5.5%)	11	(5.5%)
Herbaceous	214	28	(13.1%)	32	(15.0%)
Brush Ridge	202	23	(11.4%)	31	(15.3%)
Giant *Lobelia*	200	12	(6.0%)	11	(5.5%)
Alpine	200	7	(3.5%)	10	(5.0%)
Karisimbi meadows	200	11	(5.5%)	11	(5.5%)
Total	1974	174	(8.8%)	179	(9.1%)

Table 3.16 The misidentification of both vegetation types forming the dominant biomass of measured plots. Similar to Table 3.15 this table shows the number of cases where neither of the assigned vegetation types were dominant.

Habitat Type	Total plot number	Leaf mass		Total mass	
Bamboo	102	0		0	
Saddle	277	4	(0.7%)	1	(0.4%)
Meadow	100	0		0	
Herbaceous	107	0		3	(2.8%)
Brush Ridge	101	0		1	(1.0%)
Giant *Lobelia*	100	0		0	
Alpine	100	0		0	
Karisimbi meadows	100	0		0	
Total	987	4	(0.4%)	4	(0.4%)

Table 3.17 Duiker preferences (+) and avoidance (-) for vegetation types within a habitat determined using Chi^2 tests on the droppings counts.
* = P<0.05, ** = P<0.01, *** = P<0.001.

VEGETATION	BAMBOO	SADDLE	MEADOW	HERB.	BRUSH RIDGE	GIANT *LOBELIA*	ALPINE	KARISIMBI MEADOWS
Bamboo	- *							
Hagenia								
Crasso.								
Nettle								
Clover								
Celery								
Impatiens		+ ***						
Fern								
Solenost.		+ **		+ ***				
L.giberroa					+ *			
L.mildbr.								
Grass			- *				+ *	
Thistle								
Plectranth.								
Carex								
Hypericum								
S.mariettae					- **			
Moss								
G.Senecio							+ *	+ ***
P.kerstenii								
Alchemilla								

Table 3.18 Bushbuck preferences (+) and avoidance (-) for vegetation types within a habitat determined using Chi^2 tests on the droppings counts.
* = P<0.05, ** = P<0.01, *** = P<0.001.

VEGETATION	BAMBOO	SADDLE	MEADOW	HERB.	BRUSH RIDGE	GIANT *LOBELIA*	ALPINE	KARISIMBI MEADOWS
Bamboo	- ***							
Hagenia		- ***						
Crasso.	+ ***	- **			- *			
Nettle	+ **	+ ***			+ **			
Clover		- *						- **
Celery	+ **							
Impatiens	+ ***	+ ***						
Fern	+ ***			+ **	+ **			
Solenost.	+ ***					-		
L.giberroa					+ ***			
L.mildbr.			- ***					
Grass		+ *	+ ***				+ **	+ *
Thistle				+ *		+ **		
Plectranth.		- ***			+ **			
Carex			- ***					
Hypericum								+ *
S.mariettae					- ***			
Moss							- ***	
G.senecio							+ **	+ *
P.kerstenii			- *					
Alchemilla								- ***

Table 3.19 Buffalo preferences (+) and avoidance (-) for vegetation types within a habitat determined using Chi^2 tests on the droppings counts.
* = P<0.05, ** = P<0.01, *** = P<0.001.

VEGETATION	BAMBOO	SADDLE	MEADOW	HERB.	BRUSH RIDGE	GIANT *LOBELIA*	ALPINE	KARISIMBI MEADOWS
Bamboo								
Hagenia								
Crasso.		- ***						- ***
Nettle		- ***						
Clover		+ ***						- **
Celery				+ *				
Impatiens								
Fern	+ **			+ **				
Solenost.		- ***						
L.giberroa		- ***						
L.mildbr.			- ***					
Grass		+ ***	+ ***				+ ***	+ ***
Thistle								- *
Plectranth.								
Carex			- ***					
Hypericum								
S.mariettae								
Moss								
G.senecio								- **
P.kerstenii			- **				+ *	
Alchemilla								- **

the animal. However, during observations of these animals I never observed any obvious change in behaviour when they defaecated except for the duiker. Also the vegetation types preferred by the bushbuck and buffalo corresponded with where they were most often observed. Differences in the use of the vegetation types between the duiker, buffalo and bushbuck were examined with a one-way analysis of variance. The only significant differences were between bushbuck and buffalo in their use of the vegetation types within the Bamboo zone ($F=7.88$, d.f.=1,18 $P<0.05$) and between duiker and bushbuck in the Herbaceous zone ($F=6.28$, d.f.=1,24, $P<0.05$).

3.3.6 Herbivore preference and biomass

Table 3.20 shows the percentage use by each population of each habitat type for the transect and clearance plot counts. Bonferroni's Z-statistic was used to test which of these percentages constituted a significant preference or avoidance for a habitat (Neu, Byers, Peek & Boy 1974). The results of these tests are shown in Tables 3.21 & 3.22. Neu et al. (1974) suggest the use of $P<0.1$ level as a suitable level to assume a significant difference for this test and this explains the unusual asterisk significance levels in the tables. Elephant preference was calculated in two ways, one of which omits the habitats on Bisoke because the elephants never climbed up the steep slopes on the volcano. When this is done the elephant show no preference for any habitat.

An estimate of herbivore biomass for each habitat and species is given in Table 3.23. This table uses the mean population size estimated for the bushbuck and buffalo from the transect counts throughout the year, and the density estimated for the elephant throughout the two year study period (Table 3.10). It can be seen that despite using the conservative estimates of bushbuck density the bushbuck and buffalo dominate the herbivore biomass around Karisoke. Table 3.24 shows the total herbivore biomass and the mean density of animal mass for each habitat type. As was shown for the

Table 3.20 The percentage use of each habitat by the herbivore populations. Percentages were determined from the numbers of animals in each habitat calculated from the droppings counts. The percentage of the study area formed by each habitat is given at the bottom of the table and any values for the herbivores greater than these are indicated in bold.

	Bamboo	Saddle	Meadow	Herb.	Brush Ridge	Giant *Lobelia*	Alpine	Karisimbi Meadows
CLEARANCE PLOTS.								
Bushbuck	1.4	**60.9**	0.8	**21.9**	6.6	3.5	1.5	3.4
Duiker	0.8	**60.6**	2.2	8.5	**12.2**	4.2	2.9	**8.6**
Buffalo	**5.1**	44.0	**11.7**				0.8	**38.4**
TRANSECT ESTIMATES.								
Bushbuck								
Dec.-Feb.	2.1	**71.3**	1.3	13.8	4.3	2.5	2.0	3.4
Mar.-May	1.5	**57.3**	1.8	**23.0**	5.8	4.5	2.0	4.1
Jun.-Aug.	**2.6**	**72.5**	1.2	11.8	5.1	2.7	1.2	2.9
Sep.-Nov.	1.7	**68.1**	1.0	16.5	3.5	2.9	2.1	4.2
Mean	2.0	**67.2**	1.3	16.3	4.7	3.2	1.8	3.5
Buffalo								
Dec.-Feb.	0	51.4	**18.6**	7.3			0	**22.7**
Mar.-May	**6.6**	**60.0**	**5.5**	3.3			2.5	**22.1**
Jun.-Aug.	0	47.2	**11.3**	13.4			2.2	**25.9**
Sep.-Nov.	**7.9**	**59.9**	**9.1**	14.0			0.9	**8.3**
Mean	**3.6**	**54.6**	**11.1**	9.5			1.4	**19.8**
Elephant								
Jun.-Aug.	**5.9**	**75.7**	1.2	17.2				
Gorilla								
Wet season	**15.1**	30.0		**29.5**	**13.5**	**6.5**	5.4	
Dry season	0.7	23.4		**39.9**	**20.5**	**7.2**	**8.3**	
Mean	**7.7**	27.0		**34.4**	**17.0**	**6.9**	**7.0**	
Vegetation available.	**2.4**	**52.8**	**2.4**	**17.9**	**7.9**	**5.3**	**5.6**	**5.7**

Table 3.21 The preference by each species of herbivore censused from the clearance plots for each habitat type using Bonferroni's Z-statistic. (## = Avoidance ($p<0.05$), ** = Preference ($p<0.05$, **ns** = not significant)

Clearance plots:

Vegetation Type	Duiker	Bushbuck	Buffalo
Bamboo	ns	##	ns
Saddle	ns	**	ns
Meadow	ns	##	ns
Herbaceous	##	**	
Brush Ridge	ns	ns	
Giant *Lobelia*	ns	##	
Alpine	ns	##	##
Karisimbi meadows	ns	##	**

Table 3.22 Preferences by each herbivore for each habitat type determined from the transect counts. Preferences were calculated using the Bonferroni's Z-statistic and are given for the wet and dry seasons and the mean use throughout the year (total). The preference by elephant is calculated for the whole study area and also with the habitats up Bisoke excluded as these animals did not climb the steep slopes on this volcano.

** = Preference (P<0.05) ## = Avoidance (P<0.05)
* = Preference (P<0.1) # = Avoidance (P<0.1)
ns = not significant

	Bamboo	Saddle	Meadow	Herb.	Brush Ridge	Giant *Lobelia*	Alpine	Karisimbi Meadows
Bushbuck:								
Wet	##	**	##	**	##	##	##	##
Dry	ns	**	##	##	##	##	##	##
Total	ns	**	##	##	##	##	##	##
Buffalo:								
Wet	*	ns	*	##			##	**
Dry		ns	**	#			##	**
Total	ns	ns	**	##			##	**
Gorilla:								
Wet	**	##		**	ns	ns	ns	
Dry	ns	##		**	*	ns	ns	
Total	**	##		**	**	ns	ns	
Elephant:								
Total all study area)	ns	**	ns	ns				
Total Excluding Bisoke slopes)	ns	ns	ns	ns				

Table 3.23 The total biomass (kg) of each species of herbivore in each of the habitat types. The masses used for each species are given in parentheses and are fairly conservative.

Habitat type	Duiker (18kg)	Bushbuck (50kg)	Buffalo (325kg)	Gorilla (80kg)	Elephant (1700 kg)
Bamboo	234	418	463	79	107
Saddle	1,854	14,211	6,126	278	1,246
Meadow	68	286	1,121		19
Herbaceous	259	3,451	1,008	354	277
Brush Ridge	374	1,009		175	
Giant Lobelia	128	669		71	
Alpine	88	378	171	71	
Karisimbi meadows	265	739	2,169		
Total	3,270	21,161	11,058	1,028	1,649

Table 3.24 The total large herbivore biomass (given to the nearest ten kilograms) and the biomass density in each habitat type in the study area. The mean biomass density for the whole study area is also calculated from the total biomass of herbivores for this region.

Habitat type	Biomass (kg)	Biomass ha^{-1} (kg)
Bamboo	1,300	45
Saddle	23,720	37
Meadow	1,490	51
Herbaceous	5,350	25
Brush Ridge	1,560	16
Giant Lobelia	870	13
Alpine	710	10
Karisimbi meadows	3,170	46
Total	38,170	31

vegetation biomass, there was a decrease in herbivore biomass with increasing altitude (although there were peaks where meadows occurred).

3.4 Discussion

3.2.1 Comparison of the census techniques

The only species which were censused by both the clearance plot technique and the transect (standing crop) counts were the buffalo and bushbuck. Comparison between the buffalo clearance plot data (Tables 3.2 and 3.3) and the results of the transect counts (Tables 3.6 and 3.7) shows that the total animal density for the study area was similar at 3.4 animals km^{-2}. The only transect count that coincided with the clearance plot count was the March to May period and therefore it is quite possible that the small differences between the two methods are due to the time of the census. The clearance plot counts also suffer from low totals in the actual number of buffalo pats and hence have high standard errors.

Bushbuck numbers from the transect counts were significantly lower than the clearance plot counts although the bulk of this difference was from the Saddle zone where numbers were highest. The mean density of bushbuck in the study area from the transect counts was 34 animals km^{-2} (Table 3.5) whilst the density from the clearance plots was 52 km^{-2} (Table 3.3).

The model used in the standing crop analysis circumvents the assumption that dung levels are in a state of equilibrium (i.e. the amount of dung deposited is equal to the amount lost through decomposition). This model can also be used where dung decay does not fit a mathematical formula to give a single value as a decay rate. However, it does require dung to be monitored over a complete year to obtain an estimate of the percentage remaining after each month. For animals such as buffalo and elephant,

whose dung takes several months to disappear, this can be extended to two or three month periods but for bushbuck the dung must be monitored for every month. The use of the clearance plot technique to validate this model has shown that one of these census methods is inapplicable for censusing the bushbuck. It was possible that the habitat was opened up by the clearance of each of the plots. The recording of bushbuck and buffalo dung on paths on the transect counts showed that these animals were ten times more likely to defaecate in areas where the vegetation had been opened up. The non-random placing of the clearance plots may also have been a factor that increased this count or it may have been that the removal of dung actually encouraged bushbuck to defaecate on the plot. Dung was removed by throwing it outside the plot or grinding it to an amorphous mass and either of these may have affected the behaviour of the animals.

If the preferences for each habitat type are calculated for both census techniques (Tables 3.21 & 3.22) it can be seen that they both show similar results for the buffalo and bushbuck, indicating that it is only the magnitude of the numbers within the habitats that is at fault. For my population biomass estimates I used the conservative estimate of the bushbuck population because this correlated with the number of recognisable individuals around Karisoke and was nearer to other density estimates for bushbuck.

The bushbuck numbers fluctuated throughout the year increasing by about one quarter between March and August (Table 3.5). This increase could have been due to a seasonality in births of fawns or it could have been due to immigration into the study area. There was no obvious difference in the presence of dung at different altitudes between March to August and September to February although the fact that much of the dung will have persisted from one period to the next confounded this analysis. Any immigration of animals was likely to be due to animals coming down off the neighbouring mountains because of inclement weather conditions. Therefore if there

was no change in the use of altitude between these two periods, immigration was less likely to be the cause. However, analysis of the western and eastern parts of the Saddle zone did show a significant population increase in the west during June to August. Therefore some of the increase in the bushbuck population in the Saddle zone at this time (Table 3.4) could be attributed to migration of bushbuck into the study area across the only open boundary in the west. The main dry season (June-August) in 1988 when the transect count was done was particularly cold at night and followed an exceptionally cold and wet March to May (see Figure 2.7, B. Hastings and A. Byers in press). Most of the main streams dried up, leaving a few pools of water in the study area. Either the temperature or the lack of water could have encouraged an immigration of animals. Lack of water was probably the reason why the buffalo used the eastern half of the Saddle zone during the dry seasons, because buffalo are known to need regular access to water (Sinclair 1977). Immigration, however, cannot account for all of the bushbuck population increase between March and August because in the eastern half of the Saddle zone there was a general increase in bushbuck numbers throughout this period and this cannot be explained by immigration.

Another possibility that could explain the bushbuck population rise is that there was a seasonal period of births. During the study period all young antelope fawns and buffalo calves that could be aged as being less than about three months old were recorded whenever they were seen (except fawns of known individuals around Karisoke which were only counted once). Although numbers are small, Figure 3.4 indicates that most new young did appear between April and October for bushbuck and could therefore have contributed to this population increase. The fawns seen were past the suckling stage in most cases and therefore would have been contributing to the standing crop of dung.

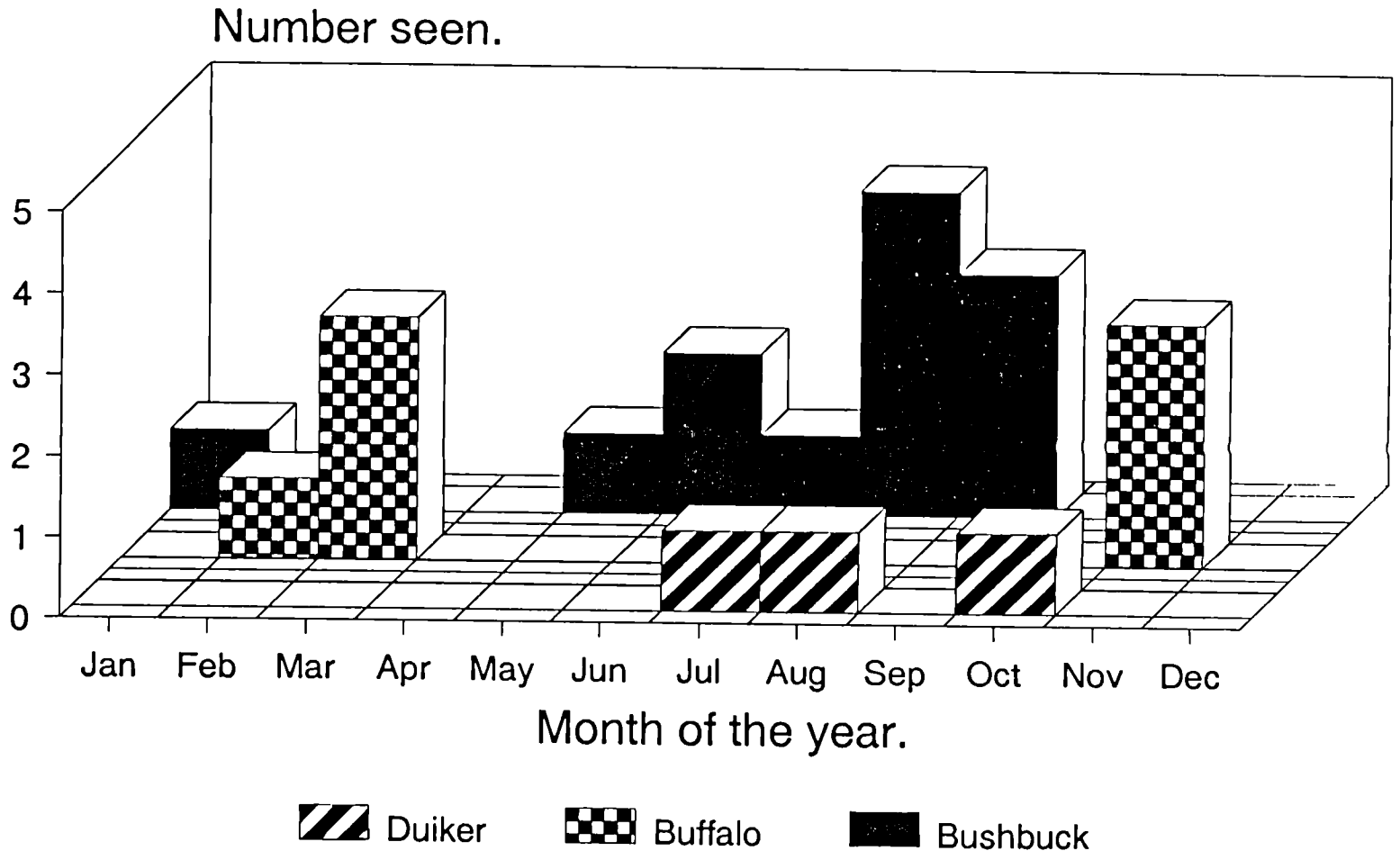


Figure 3.4 The number of young bushbuck, duiker and buffalo observed at different months of the year. A young animal was defined as one that could not be more than about three months old

3.4.2 Herbivore densities

Tropical rainforest is not a habitat that normally encourages a high density of large terrestrial herbivores. Typically most species of Artiodactyla or Perissodactyla in the tropics are adapted for open habitats where grasslands predominate. Mature forest contains a high biomass of plant material but most of this is locked up in the cellulose contained in the trunks of trees and is not available to the animals as food. Most plant food is to be found in the canopy where primates and edentates are the main mammalian groups to use this resource (Eisenberg & McKay 1974).

The Birungas, however have a comparatively high biomass of herbaceous vegetation available to terrestrial herbivores which would allow a higher biomass of mammalian herbivores to be sustained. The estimates of animal densities are compared with other estimates of the same or similar species elsewhere in forested habitats in Table 3.25. The gorilla density around Karisoke is one of the highest values recorded for any forest but this was biased by the fact that this region was chosen in the first place because it was a good area for these animals. The results of the 1989 mountain gorilla census produced a minimum estimate of 306 animals in the whole park (i.e. a mean density of 0.72 gorillas km^{-1}). The mean density of elephant for the study area for the whole study period would be equivalent to about 30 animals throughout the park. During the 1989 mountain gorilla census the only signs of elephant were in the region between Sabinyo and Bisoke on the Zaire side of the park. It is possible still for elephant to migrate between the savanna Virunga park in Zaire and the forest (C. Aveling pers. comm.) and this may be important if this small population is to survive. The Buffalo density in Table 3.25 is lowest around Karisoke but this is because all the other measures come from savanna or woodland habitats. The mean figures from the two meadow types of 9.6 (Karisimbi meadows) and 11.8 (meadows) are probably more comparable with these densities.

Table 3.25 A comparison of the densities of the species of herbivores studied here and the same or similar species studied elsewhere.

Species Location.	Habitat	Density (Km^{-2})	Source
Duiker:			
Hyemoschus aquaticus	rainforest	7.7-28.0	Dubost 1978
Cephalophus callipygus	rainforest	25.0	Dubost 1979
Cephalophus monticola	rainforest	62-78	Dubost 1980
Red duiker, Ituri.	rainforest	49-81	Wilkie & Finn 1990
Cephalophus nigrifrons	montane forest	14	This study
Bushbuck: *Tragelaphus scriptus*			
Ruwenzori park	woodland	26	Waser 1975
Nairobi park	savanna	30.1	Allsopp 1978
Sengwa valley	savanna	66.7	Jacobsen 1974
Karisoke	montane forest	34.4	This study.
Buffalo: *Syncerus caffer*			
Mt. Meru	montane meadow	22.8	Sinclair 1977
Manyara	woodland	17-21	Sinclair 1977
Virunga park, Zaire	savanna	12.3	Sinclair 1977
Serengeti (north)	savanna	7.4	Sinclair 1977
Serengeti (south)	savanna	3.6	Sinclair 1977
Karisoke	montane forest	3.4	This study
Gorilla: *Gorilla gorilla*			
G.g.gorilla:			
C.A.R.	rainforest	0.89-1.45	Carroll 1988
Gabon	rainforest	0.18	Tutin & Fernandez 1984
G.g.graueri:			
Masisi, Zaire	rainforest	0.83	Yamagiwa *et al* 1989
Kahuzi-biega	montane forest	0.37	Murnyak 1981
G.g.beringei:			
1963, Birungas	montane forest	1.15	Schaller 1963
1989, Birungas	montane forest	0.72	Recent census
Karisoke	montane forest	1.10	This study
Elephant: *Loxodonta africana*			
Congo	rainforest	0.06	Douglas-Hamilton 1987
Murchison (north)	riverine	0.47	Douglas-Hamilton 1987
Murchison (south)	riverine	0.01	Douglas-Hamilton 1987
Ivory coast	rainforest	0.03-0.2	Douglas-Hamilton 1987
Sierra Leone	rainforest	0.23	Merz 1986
Ghana	rainforest	0.33	Short 1983
Kilimanjaro	montane	0.15-0.67	In:Ruggiero 1989
Karisoke	montane forest	0.10	This study

Table 3.26 Mammalian herbivore biomass density in various habitats throughout the world. Values are obtained from Botkin *et al.* (1981) for all habitats except the Lope reserve which was provided by L. White (pers. comm.).

Location	Habitat	Biomass (Kg ha^{-1})
Murchison Falls	Riverine	280
Serengeti	Savanna	87
Tsavo	Grass/bush	45
South Dakota	Prairie	36
Karisoke	Montane forest	31
Lope reserve	Primary rainforest	25
Isle Royale	Temperate woodland	7
Michigan	Woodland	7

3.4.3 Herbivore biomass

A comparison of the region around Karisoke and other ecosystems is given in Table 3.26. Considering that the climatic conditions found in the Birungas are more similar to a temperate ecosystem, it is surprising to find that Karisoke sustains the highest biomass of large herbivores for any forest yet studied. The masses used for each species of animal in this measure were some of the most conservative of the masses given in the literature. For instance the mass of a buffalo was taken as 325kg rather than the 450kg sometimes used which is the mass of an adult buffalo but ignores the fact that part of the population is composed of calves and juveniles. Similarly a smaller mass for elephant has been used because the elephant in the Birungas appear to be the smaller forest subspecies, *Loxodonta africana cyclotis*, or intermediates between forest and savanna elephants (R. Barnes pers. comm.). It has been shown that measurements of footprint size can be related to shoulder height in elephants (Western & Moss 1983). The largest animal that I was able to measure in this way was 200cm at the shoulder, about 50cm shorter than an adult female in Amboseli National park and 100cm shorter than a large bull.

Sukumar (1989) gives biomass estimates for herbivores in India's forest parks as between 3.8 and 12.6kg ha^{-1}. If domestic animals are included in the estimate, however, this figure is elevated to between 53 and 64kg ha^{-1}. One of the problems with many of these estimates is that domesticated animals or the smaller mammals are not included because they were not part of the study. Rodents and tree hyrax (*Dendrohyrax arboreus*) are numerous in the study area, dung being found as high as 3700m at the summit of Bisoke. These species could make an important contribution to the total biomass. Verschuren (1966) gives the following rodent biomasses in the Birungas: Bamboo 0.2kg ha^{-1}; Hagenia-Hypericum woodland 2.2-3.2 kg ha^{-1}; Herbaceous 1.8kg ha^{-1}; Alpine 1.2kg ha^{-1}. These figures will therefore only change the overall estimate of 31kg ha^{-1} by about 1kg. If it is assumed that there is one hyrax

in every second *Hagenia* tree (a not unreasonable estimate) then the density of *Hagenia* trees from the vegetation survey can provide an estimate of hyrax biomass. If the average hyrax is 3kg (Sinclair 1975) then the biomass contribution of these animals could be as high as 60kg ha^{-1} in the Saddle zone, almost double the biomass of the large herbivore population. Even if this was the only habitat type that contained this species the mean biomass per hectare for the whole study area would be higher than the large herbivore biomass of 31kg ha^{-1}. Cheeseman (1975) suggested that a low biomass of rodents in Uganda can still have a significant impact on the available vegetation because of the way they consume their food, some biting off blades of grass near the base and only consuming a small proportion. Senzota (1984) gives a figure of 80% of clipped grass being wasted by rodents in the Serengeti. During certain seasons insect biomass has also been shown to have an appreciable effect on the vegetation in the Serengeti because of similar wastage of clipped vegetation, a grasshopper destroying about 1.5 times its body weight each day (Sinclair 1975). Therefore when investigating total biomass of animals in different ecosystems it is important to consider all species since even the smallest can be of some importance to the functioning of the system.

Four of these five herbivores showed some degree of selective use of the eight habitat types designated, and each species selected habitats that were not preferred by the other herbivores. Gorillas, for instance, were the only herbivore to prefer the herbaceous zone all year round, whilst buffalo were the only herbivore to prefer the two meadow types (Table 3.22). Hence there appears to be some degree of separation of these herbivores in their use of the available habitat and this could be of importance in the maintenance of the large biomass density in this forest. This niche separation could enable different species to coexist within the same ecosystem and this is investigated further in the context of the Birungas in Chapter 6.

CHAPTER 4.

THE UTILISATION OF THE AVAILABLE HERB BIOMASS BY THE LARGE MAMMALIAN HERBIVORES IN THE BIRUNGAS.

4.1. Introduction.

The second resource dimension that is of importance in niche separation is the differential use of the plant species as a food resource (Schoener 1974). By feeding selectively on certain plant species or certain plant parts the potential for competition between herbivores can be reduced. Studies on the feeding ecology of herbivores can also shed light on the factors which control their populations.

As the herbivore populations around Karisoke experience little poaching and predation pressure is low, something else must eventually limit the continual growth of their populations. The most likely resource that will be limiting is food supply. Whilst ecologists would agree that most animal populations are resource limited (White 1978), few would agree that there is a shortage of food plants. Therefore not all plant material can be considered as food and this indeed has been found in several studies. Sinclair (1977) showed that during the dry season in the Serengeti the nitrogen content of grass species was below that required by buffalo to maintain body condition and this caused increased mortality of the old and young animals. McNaughton *et al.* (1985) showed that grasses in regions that were heavily grazed contained higher concentrations of silica which can be detrimental to herbivores in several ways, one of which is to increase tooth wear (Baker, Jones & Wardrop 1959). Many plant species also contain defensive chemicals in their leaves or shoots (so called secondary compounds) which have various effects on herbivore digestion (Freeland & Janzen 1974, Rhoades 1985). For example, Waterman *et al.* (1980) showed that tannins reduced the digestibility of African rainforest vegetation to

ruminants. Cates & Orians (1975) however, found that herbaceous vegetation such as that in the Birungas is less likely to be defended by alkaloids, tannins or other secondary compounds. It is the slow growing plant species which are part of the late successional climax community that tend to invest in these defences. Furthermore, the investment by plants in defence in relation to investment in growth is likely to decrease with increasing temperature stress (Van Soest 1982) and hence is likely to be lower in the Birungas. Watts (1983) looked for condensed tannins, alkaloids and phenolics in mountain gorilla food plants and found that they were indeed very low when compared with other African rainforests. Since much of the herbaceous vegetation would appear to be available to herbivores as a food source, what factors are limiting the herbivore populations in the Birungas?

To answer this question the diets of each of the herbivore species must be determined. The intake of plant species by herbivores has been calculated in various ways depending on the type of study and the applicability of the techniques available. Probably the most accurate technique is to use oesophageal fistulas which remove the plant items as they are eaten (Van Dyne & Torrell 1964). This method, however, requires tame animals and cannot easily cover the variability that will exist in the choice of food by different animals. Watts (1983) showed that individual mountain gorillas could have quite different diets even when they were living within the same group and visiting the same food supply. If it is possible to observe an animal, individual bites can be recorded (Dunham 1980, Watts 1984) and bite size related to biomass ingested. Other studies have been more interested in the total plant biomass removed, rather than the biomass of the individual species consumed, and have studied offtake using exclosure plots where the environment is fairly uniform (McNaughton 1985). In the case of browse offtake it is possible to visit areas after an animal has fed and relate measures of twig or stem dimensions to the biomass of plant material removed (Barnes 1976). Although a variety of techniques have been

tried, the most commonly used technique is the microscopic analysis of plant remains in rumen, stomach or faecal material.

Many plants can be identified to the species level by characteristics of the leaf epidermis which can be identified on the plant cuticle (Stewart 1965, 1967). Faecal analysis has the advantage over other techniques in that it can easily cover the variation that exists within a species, it does not require dead or tame animals and it does not interfere with the normal habits of the animals. In this study it was the only technique possible as the vegetation was too dense to observe the animals and no cull material was available.

There are, however, several disadvantages to faecal analysis (Holchek, Vavra & Pieper 1982, Gill *et al* 1983). The first of these is that accuracy can be a problem if the forage remains in the faeces are not proportional to the species consumed. If some plants are digested more than others then this would occur. Secondly it is not possible to tell where the plant species were eaten, and so measuring dietary preference can only be done on a broad scale. Thirdly, some species of plant fragment more readily than others and usually it is only the largest fragments that can be identified. This means that there is a bias towards those species that have the largest fragments and hence can be identified more easily (Norbury 1988).

One further problem that had to be overcome for this study is that the digestive systems of the animal species vary widely, and in fact cover most of the potential variability in mammalian herbivores. The mountain gorilla and the elephant are hindgut or caecal fermenters whereas the others are ruminants. Caecal fermenters tend not to digest forage as well as ruminants because they are adapted to cope with poor quality diets, usually high in fibre. This means that they tend to eat more food and process it quickly, extracting the nutritious components but passing the rest. Ruminants on the other hand have evolved to retain food for longer in the rumen,

extracting more of the available nutrients (Demment & Van Soest 1985). Hofmann (1973, 1989) has also shown that there is much variation between ruminant species, both in stomach structure and feeding ecology. Ruminants can be placed into three categories; concentrate selectors, intermediate mixed feeders and bulk and roughage feeders. Concentrate selectors such as the bushbuck and black-fronted duiker feed selectively on highly nutritious and digestible plant parts and therefore they do not need to reduce the rate of passage through the gut. At the other extreme the bulk and roughage feeders such as the buffalo have a complex filtering system that retains a poorer quality and less selective diet in the rumen for longer allowing time for digestion to extract the available nutrients. Poppi, Henderson & Minson (1985) have shown in cattle that any plant particles greater than 4.75mm fail to pass through the filtering mechanism in the omasum. Therefore if any of the herbivores in the Birungas were eating the same plants, the extent to which each species is broken down could vary considerably.

Although there are these problems with faecal analysis, the effects can be minimised by analysing the faeces in particular ways and applying correction factors. In this study it was the only technique that could be applied and this chapter describes how these problems were overcome.

4.2 Methodology

4.2.1 Collection

Faecal material was collected for each species in each habitat type they frequented. At least 15 samples of approximately equal size were collected from fresh defaecations (not more than a couple of days old) at monthly intervals as suggested by Anthony & Smith (1974). It was not always possible to find enough fresh

defaecations in each habitat type for each month and therefore the dung was combined by seasons. Only those habitat types very rarely used by an animal failed to meet this requirement even when the material was pooled. Faecal material was preserved in 10% formalin and flown back to Bristol for analysis.

4.2.2 Nutrient analyses

Faecal material was also collected from the Saddle zone (because it was the largest and most representative habitat type), dried by a charcoal burning stove and sealed in a container for the estimation of faecal nitrogen content. Faecal nitrogen has been shown in several studies to be correlated with dietary nitrogen intake and hence can give a measure of the quality of the diet (Erasmus, Penzhorn & Fairall 1978, Leslie & Starkey 1985). Green leaves of the main plant species in the study area were also collected and dried for analysis of nitrogen content, mineral concentrations and digestibility. This involved collecting at least 100 plant leaves of varying ages and from different sites in the study area. This ensured that variations due to soil nutrient status, plant competition or age of the plant did not bias the analysis. Material from some of the major plant species was collected both in a wet and a dry season separately to examine for any major variation between seasons. Nitrogen and, for some plant species, phosphorus were determined in a kjeldahl digest solution following the method of O'Neill & Webb (1970). Mineral content was analysed using an atomic absorption spectrophotometer, cellulose digestibility according to Choo *et al.* (1981) and ash content by drying at 375°C (Baines 1990). Mineral content, digestibility and ash content were analysed by Charles Baines for his final years project, to whom I am indebted.

4.2.3 Preparation of faeces

In order to compensate for differential digestion between herbivores, faecal material was broken up gently by grinding in water (elephant and gorilla faeces had to be put in a homogeniser initially to break up the fibrous material), washed several times in water to remove the formalin and then digested in pepsin (600mg in 300ml 0.1M HCl) for 24 hours followed by cellulase (1.875g cellulase (*Trichoderma viridae*) with an activity of 0.02EU/mg in 300ml citrate/phosphate buffer of pH 4.6) for 48 hours at 40°C. Pepsin and cellulase have been used as a means of determining plant digestibility (Jones & Hayward 1975, Choo *et al.* 1981). Wilson, McLeod & Minson (1989) showed that grass particles fragmented most within the first 24 hours in the rumen of a cow, and after 96 hours very little fragmentation occurred. Therefore by digesting the dung for a further 72 hours it is likely that most differences in the degree of fragmentation of plant species between herbivores will be eliminated. This is because all plants will have had at least 24 hours in the guts of the herbivore and, after a further 72 hours digestion, will have shown the bulk of their decrease in size. There may still be some variation dependent on the effects of chewing by each herbivore but the homogenising of the faeces of the caecal fermenters was designed to reduce such differences between these animals and ruminants.

In order to investigate the degree of digestion by each of the herbivores, faecal material was dried to constant weight and then digested in pepsin and cellulase as above. Then it was dried again to constant weight to record the degree of further digestion that was possible.

Many studies have placed faecal material in acids (Dunnett, Harvie & Smit 1973) or bleach (Green 1987) to clear the plant cuticles of adhering epidermal tissue. It was found, however, that washing the faecal material in water after digestion in pepsin and cellulase was sufficient. The use of acids might have an appreciable effect by

reducing the size of the cuticles and hence biasing the analyses. Norbury (1988) found a significant effect of bleaching faecal material before analysis on the relative proportions of plants identified in the faeces.

4.2.4 Cuticle measurement

The faecal material was then placed on two microscope slides and four transects of each slide traversed, measuring the area of the cuticles present using a graticule. Cuticles were identified at x100-x400 magnification to species level where possible using a reference collection of photomicrographs of plant cuticles. This reference collection was made initially at Karisoke by scraping samples of leaf with a scalpel, removing the tisue until only the cuticle remained and then they were photographed in Bristol. Cuticle fragments unidentifiable at the species level were placed into groups which contained similar cuticular patterns. Cuticle characteristics used to identify species were similar to those used by Nugent (1983) and were based on cell shape, trichomes, cuticle thickness and stomata. The density of the faecal material per slide meant that at least 100 graticule squares were counted for each traverse of the slide. The estimates of the cuticle proportions for the eight transects for each sample were jackknifed as suggested by Seber & Pemberton (1979) to obtain a jackknifed mean for each species or group. "Jackknifing" is a mathematical technique that can remove the bias inherent in the calculation of proportional data when each of several estimated proportions is based on a different total sample size (in this case where the total area measured for each transect varied).

Faecal material found in a habitat may not contain food eaten in that habitat because of the movements of the animals and the fact that the habitats are used in different proportions. Therefore diets calculated from dung found in each habitat type were weighted by the proportional use of that habitat by the animal species in question and then combined into an overall diet.

4.2.5 Correction factors

Some studies using faecal analysis have attempted to correct counts of plant cuticles for differential digestion (Putman 1984). This assumes that a change in mass following in vitro digestion is proportional to a loss in cuticle. However it is easy to envisage a situation where there are two species of plant with similar cuticles but one has a much thicker leaf. Digestion of these two species would show a greater loss of mass in the thick leafed plant (assuming a similar ratio of fibre) which would give a greater correction factor even if the cuticles were digested to the same extent in both plants. To look at this problem a $1cm^2$ punch was used to collect leaf samples from a variety of plant species in the park in order to determine the mass of leaf material per unit area of cuticle. The results of this are summarised in Table 4.1, which shows that there is up to a five-fold difference in mass for the same area of cuticle. Hence it was doubtful whether correcting the diets of the animals for differential digestibility would have been valid.

Instead it was decided to correct the cuticle counts by the identifiable proportion of cuticle (Norbury 1988) that occurs after 24 hours digestion in pepsin and 72 hours in cellulase, using the same concentrations described above. Gill *et al.* (1983) and Norbury (1988) argued that the ratios of identifiable to unidentifiable fragments may also be a more important source of error. Plant material was ground through a $1mm^2$ mesh and then digested at 40°C. For each plant species the area of identifiable (at the species and at the plant group levels) and unidentifiable cuticle was measured and recorded separately. Norbury (1988) found a great improvement in the prediction of known diets when using the ratio of identifiable to unidentifiable fragments as a correction factor. A test of this technique was obtained by combining several $1cm^2$ punched leaves of two or three different species of plant to give a known ratio of

Table 4.1.
The variation in biomass of leaf material per unit area calculated from 1cm^2 samples.

Plant species	Sample number	Mass (g cm^{-2})
Lobelia giberroa	210	4.14×10^{-3}
Rubus spp.	200	6.94×10^{-3}
Galium spp.	30	2.57×10^{-3}
Peucedanum linderi	200	4.58×10^{-3}
Impatiens spp.	400	2.49×10^{-3}
Solenostemon sylvaticum	200	3.17×10^{-3}
Carduus nyassanus	210	3.33×10^{-3}
Crassocephalum ducis-aprutii	200	3.31×10^{-3}
Laportea alatipes	210	3.61×10^{-3}
Droquetia iners	150	2.66×10^{-3}
Girardinia bullosa	57	6.49×10^{-3}
Gynura ruwenzoriense	200	3.00×10^{-3}
Helichryssum globosum	100	6.05×10^{-3}
Hydroctyle spp.	150	1.50×10^{-3}
Plantago palmata	150	1.99×10^{-3}
Ranunculus spp.	150	2.64×10^{-3}
Cardamine obliqua	150	3.08×10^{-3}
Rumex bequaertii	150	2.49×10^{-3}
Parochetus communis	300	1.54×10^{-3}
Carex simensis	100	4.29×10^{-3}
Carex bequaertii	200	6.23×10^{-3}
Festuca engleri	161	4.05×10^{-3}

cuticle area for each of three different mixtures. After digesting these test mixtures and examining them under a microscope as above, the measures of the cuticle area for each species in the test mixture were corrected by the proportion of identifiable fragments obtained above. These corrected figures were then compared with the expected figures given the known area of cuticle for each species.

Certain plants could only be identified to species level if a trichome was present on the cuticle. The fragments of cuticle that did not show this trichome were placed in a group with other species. The correction factor obtained above, however, corrects the measure of the area of cuticle with trichomes to a total area. Therefore the ratio of plant cuticles identifiable at the species level to the plant group level was used to remove the portion of a particular species in the plant group designation because it was already corrected for at the species level. Finally the relative areas of cuticle obtained after correction were transformed into relative biomasses using the data of leaf mass per unit area from Table 4.1. Plants that were not measured were given a value similar to a plant of similar type in this table.

The proportion of stem intake was determined for buffalo and elephant by following trails and measuring the diameter of browsed stems at the browsing point. This measure was then related to biomass of stem and leaf through regression equations (Appendix 4). The proportion of stem to leaf material for each plant species was used to correct the diet to include a measure of stem intake. This was also done for gorillas using data for stem intake from Watts' thesis (1983). These data were first corrected to dry weight intake using the water content data from Watts (1983); water content shows no significant seasonal variation (D. Watts pers.comm.). It was assumed that bushbuck and duiker ate insignificant amounts of stems of tall herbs because I never observed any signs of such browsing.

At the same time records of the height at which plants were browsed were recorded for the buffalo and elephant and these were compared with observational data from the bushbuck and duiker. These data were recorded by 20cm intervals, the measurements being confirmed by visiting observed feeding sights after the animal had left, and were collected in the Saddle zone where the greatest variation in browsing heights was available.

4.3 Results

4.3.1 Correction factors

The correction by the identifiable proportion of fragments certainly improved the estimate of the animal diets as shown from the results of the hand compounded diets (figure 4.1). However the correction was not perfect as the estimates for two species were out by over 10%. These two species, *Impatiens* spp. and *Carduus nyassanus,* were only identifiable by trichomes and spines respectively and therefore required large correction factors. It was likely that the correction factors were less accurate when the proportional change was great because the number of identifiable fragments used to obtain the correction estimate was low. Some cuticle may also have been digested by the pepsin and cellulase rather than fragmented as was assumed. The correction factor for the *Impatiens* was changed using this hand compounded result before the diet was calculated because the cuticle for this plant is thin and may be digested. The *Carduus nyassanus* result is probably somewhat biased by the fact that the $1cm^2$ punch was not placed at the edge of the leaf where the spines are to be found and hence fewer particles could be identified than might have been expected. These two plants were the only two to require large correction factors but since they were thought to be important in the diets of each herbivore they were recorded separately.

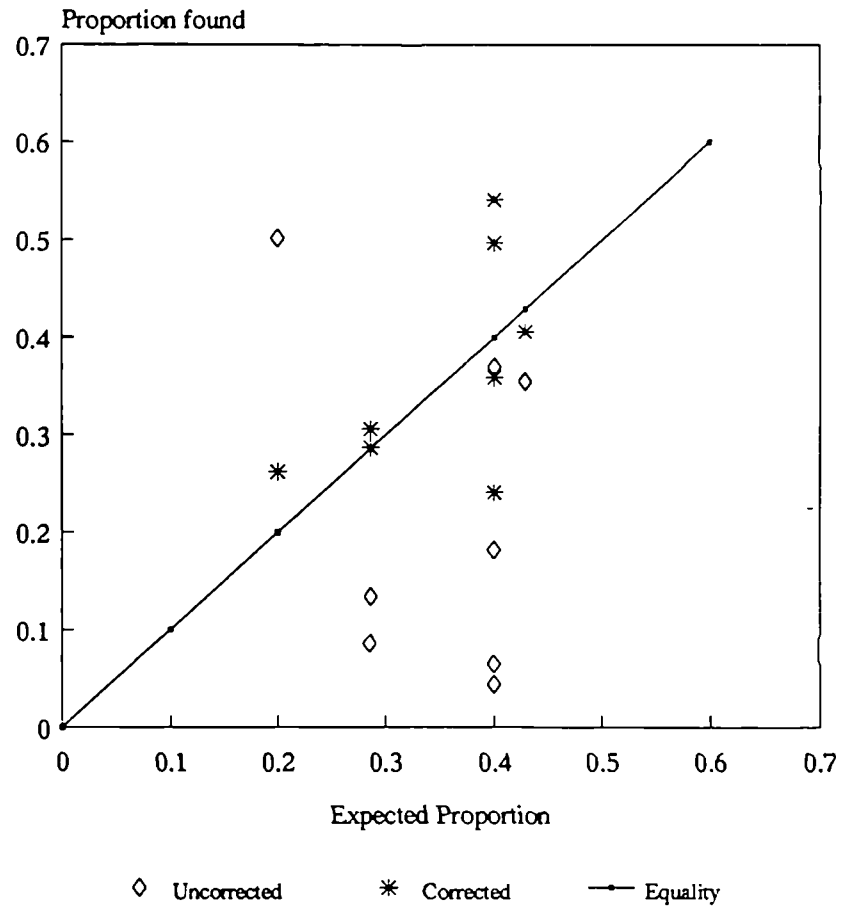


Figure 4.1 The effect of correction factors for certain plant species when applied to test samples of mixed plant species digested in vitro. The correction factor in theory should change the measured proportion obtained from microhistological analysis to the expected proportion and should move the points measured on the graph onto the line of equality. Whilst the corrections are not perfect they certainly improve the estimate.

Table 4.2
The percentage loss of matter from faeces after 72 hours digestion in pepsin and cellulase solutions and tests of the difference between species (n=5 for each species).

Animal species	Season	Percent loss	Standard error
Duiker	June	10.57	1.17
Bushbuck	May	14.27	0.81
Buffalo	May	4.59	0.89
Gorilla	May	9.14	1.36
Elephant	November	3.27	1.06

T-TEST RESULTS BETWWEEN THESE MEANS

Species	Bushbuck	Buffalo	Gorilla	Elephant
Duiker	*	**	ns	*
Bushbuck		***	*	**
Buffalo			*	ns
Gorilla				*

(ns=not significant, *=P<0.05, **=P<0.01, ***=P<0.001)

Table 4.2 shows the results of the effect of continued digestion on the faecal loss of dry mass. It shows that there is a significant difference in the loss of weight between most of the herbivores and hence the digestive efficiencies of these species do vary. It is the concentrate selectors, the bushbuck and duiker, that showed the greatest change rather than the caecal fermenters, as might have been expected. This may be because elephant and gorillas will be ingesting a greater fibre content in their diet and this will be more resistant to digestion. Janis (1976) stated that in general caecal fermenters are 70% as efficient as ruminants at cellulose digestion.

4.3.2 Diet composition

Table 4.3 shows the mean percentage intake throughout the year of each plant species (see Appendix 1 for full specific names) or plant groupings calculated for each animal species. These data are also summarised in terms of plant types in figures 4.2 to 4.6. These pie charts do not include the stem intake from tall herbs of the three largest herbivores which are as follows: Buffalo - 6.0%; Gorilla - 31.7%; Elephant - 51.4%.

Variations between seasons in the diet of each herbivore were significantly different when tested using Friedmans analysis of variance (Duiker: X^2=129.0, d.f.=37, P<0.001; Bushbuck: X^2=122.2, d.f.=37, P<0.001; Buffalo: X^2=124.0, d.f.=37, P<0.001; Gorilla: X^2=111.4, d.f.=37, P<0.001). Differences between wet and dry seasons were less significant but all were significant at the P<0.05 level. Whether this variation is real is debatable as there was no obvious change in the vegetation throughout the year. The movement patterns of the gorilla groups through their home range meant that for some seasons they never visited areas where faeces had been collected previously and this would have contributed to this difference between seasons. Figures 4.7 to 4.10 show the seasonal variation between plant types in the diet, rather than individual species, and these show no significant seasonal change.

Table 4.3 The percentage intake of food-plant species or plant species groupings by each of the five herbivores. These data were obtained from microhistological analysis of faecal samples (See text). The percentage availability by mass of the same plant species in the study area is also given, taken from the data in Chapter 2.

Plant species	Duiker	Bushbuck	Buffalo	Gorilla	Elephant	Available
Galium	3.8	1.4	1.8	20.0	1.0	1.27
Laportea	0.1	9.7	0.0	14.7	11.2	8.09
Carduus	5.1	3.9	0.0	29.2	10.6	7.62
Impatiens	20.9	17.8	4.6	0.1	0.0	1.98
Solenostemon	2.1	17.5	0.0	0.0	0.3	7.22
C.simensis	0.3	3.5	15.9	0.4	2.2	3.41
C.bequaertii	0.0	2.3	19.3	0.1	12.9	1.52
C.erythrorr.	0.4	0.7	18.1	0.0	0.0	3.72
Mariscus/ Panicum	0.0	3.4	0.4	0.0	0.0	0.45
Arundinaria	0.0	0.4	0.8	1.4	3.9	0.01
Agrostis/ F.Schimper.	11.7	20.6	14.9	0.0	0.0	1.52
F.engleri	2.4	2.5	11.9	0.0	0.0	2.20
Crassoceph.	0.0	1.5	0.6	0.0	0.1	11.23
Hypericum	0.3	0.5	0.0	0.0	0.1	0.06
Plectranthus	0.3	0.1	0.0	0.0	0.0	2.62
Rubus	0.1	1.7	0.0	1.5	0.3	0.09
Selaginella/ Moss	3.0	2.7	0.5	0.1	0.0	2.69
Fern	0.0	0.0	0.0	0.0	0.2	-
Pilea	6.1	0.0	0.0	0.1	0.0	0.89
Cerastium/ Stellaria	6.2	1.3	0.9	0.1	0.0	0.38
Luzula	0.4	0.9	0.3	0.0	0.0	0.37
Alchemilla/ Ranunculus	3.5	2.7	0.2	0.0	0.0	0.90
P.communis/ Oxalis	1.6	0.0	0.0	0.0	0.0	0.26
Gynura/ Stachys	0.7	0.3	0.0	0.1	0.1	0.34

Table 4.3 (continued)

Geranium/ Droquetia	0.9	0.1	0.0	0.3	0.1	0.08
Hydroctyle/ Hyp.peplid.	0.0	0.2	0.0	0.1	0.0	1.97
Mentha	1.9	0.1	0.1	0.0	0.0	0.08
P.linderi/ Oenanthe	0.4	1.5	3.0	0.0	0.1	1.29
Viola/ Tylophorops.	4.7	0.5	0.5	0.1	0.1	0.36
Alch.john/ Helichrysum	1.8	0.3	0.2	0.0	0.0	1.30
Lob.giberr/ Echinops	0.0	0.0	0.0	0.0	3.6	8.27
Polygonum/ P.kerstenii	0.2	0.1	0.0	0.0	0.0	0.25
Plantago/ Trifolium	1.6	0.8	0.2	0.0	0.0	0.01
Stephania/ Urtica/Girar.	0.0	0.0	0.0	0.0	2.2	1.08
Lichen	14.8	0.6	0.0	0.0	0.0	-
Stems:						
P.linderi	0.0	0.0	5.7	16.1	1.2	2.30
Carduus	0.0	0.0	0.0	8.6	25.3	3.21
Laportea	0.0	0.0	0.0	5.9	23.2	20.95
Solenostemon	0.0	0.0	0.0	0.0	0.8	-
Bark/root	4.5	0.2	0.3	1.1	0.9	-

Duiker diet

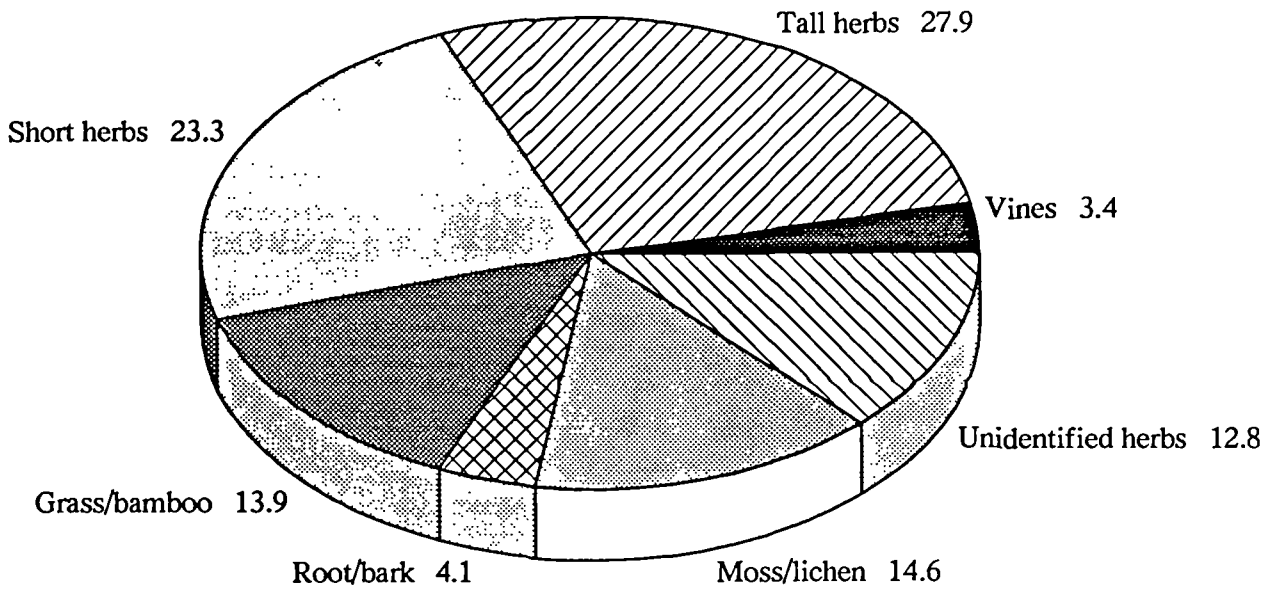


Figure 4.2 The proportion (by mass) that major plant types form in the dietary intake of the duikers in the study area. Figures are based on a yearly mean of the values obtained from microhistological analysis for each season.

Bushbuck diet

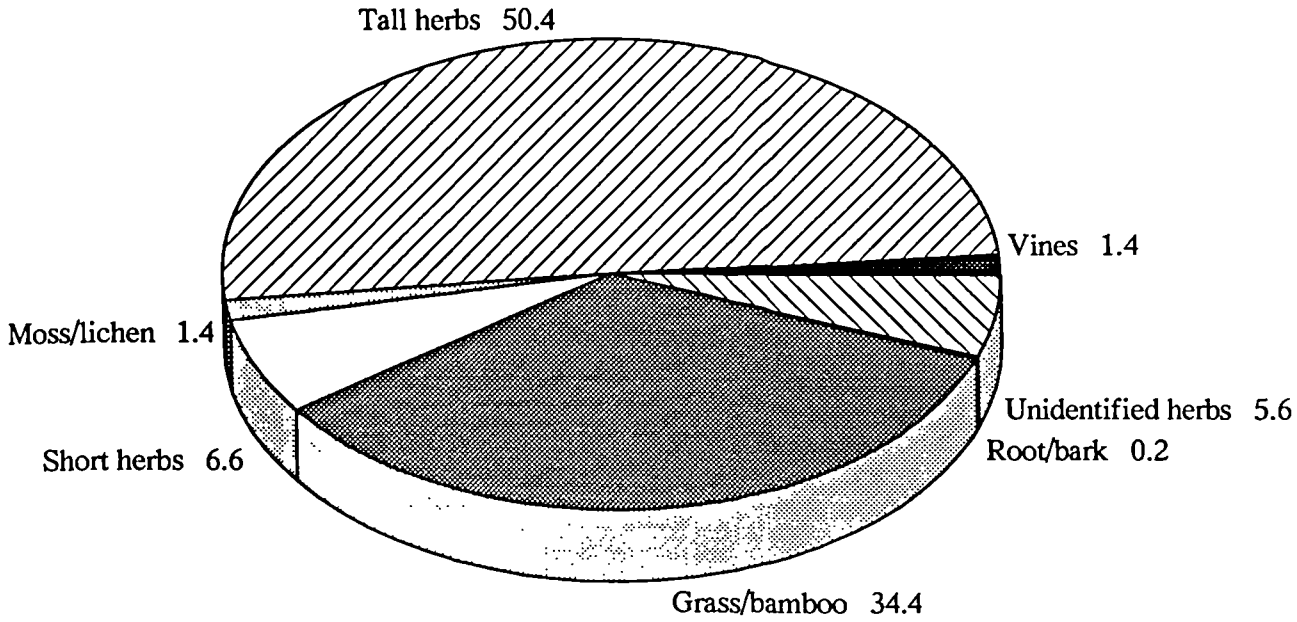


Figure 4.3 The proportion (by mass) that major plant types form in the dietary intake of the bushbuck in the study area. Figures are based on a yearly mean of the values obtained from microhistological analysis for each season.

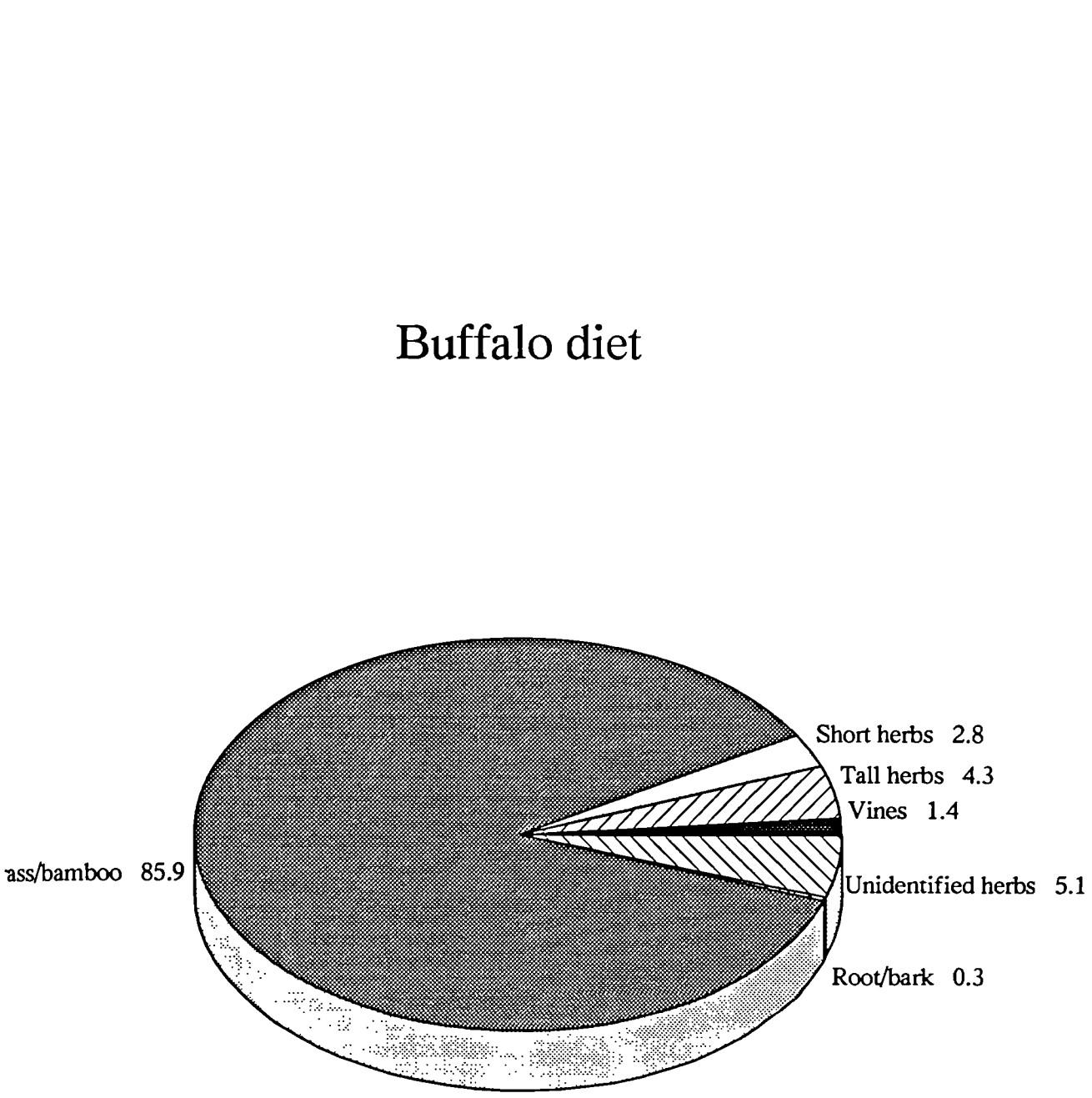


Figure 4.4 The proportion (by mass) that major plant types form in the dietary intake of the buffalo in the study area. Figures are based on a yearly mean of the values obtained from microhistological analysis for each season.

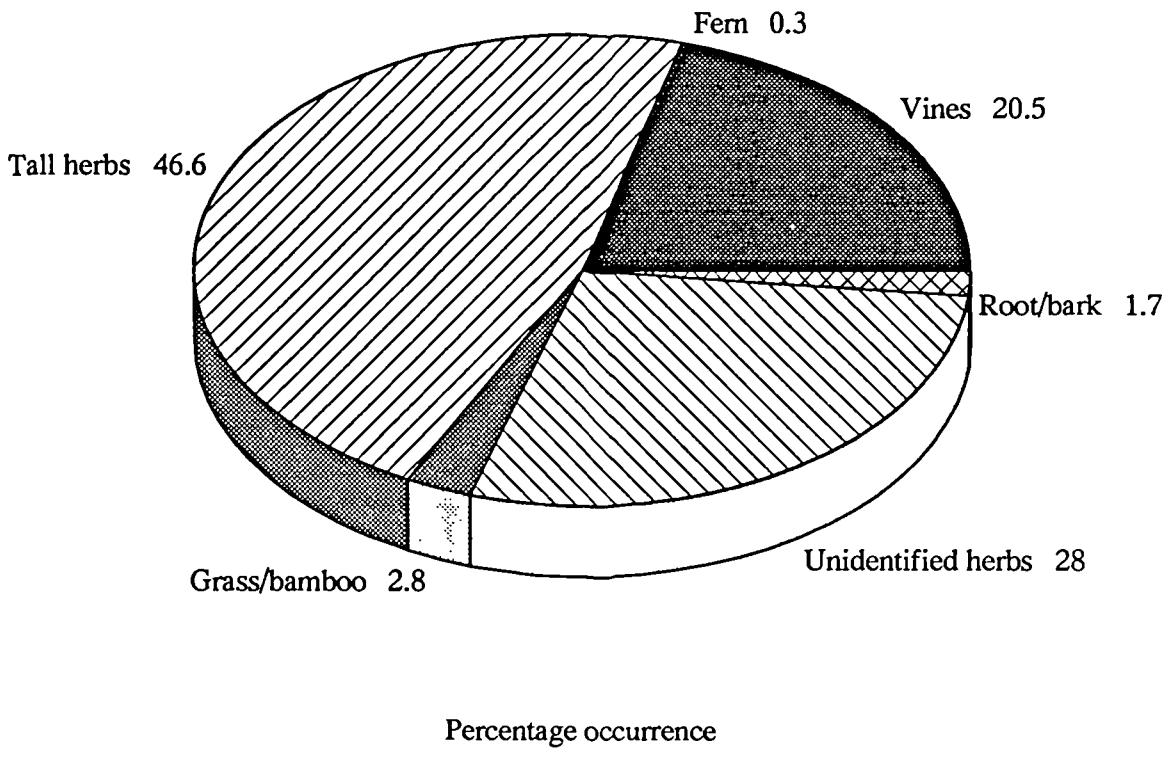


Figure 4.5 The proportion (by mass) that major plant types form in the dietary intake of the gorillas in the study area. Figures are based on a yearly mean of the values obtained from microhistological analysis for each season.

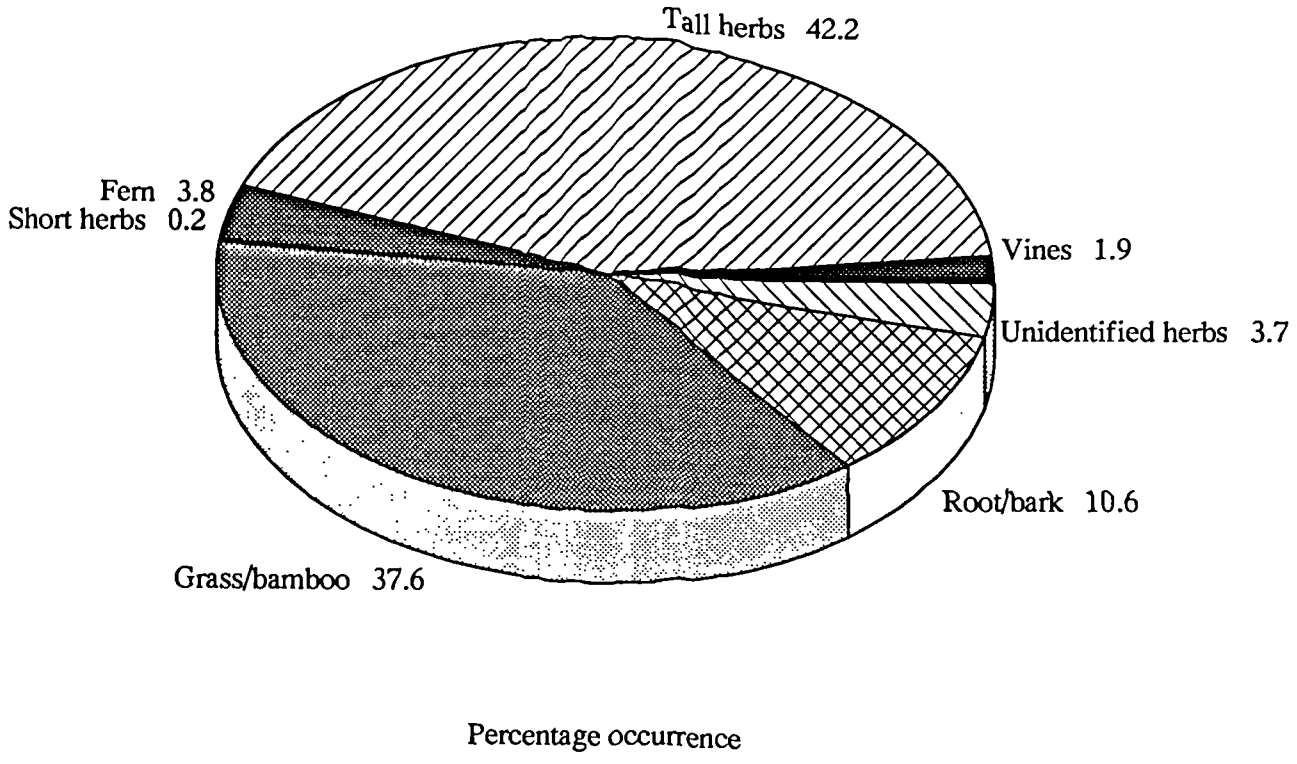


Figure 4.6 The proportion (by mass) that major plant types form in the dietary intake of the elephant in the study area. Figures are based on a yearly mean of the values obtained from microhistological analysis for each season.

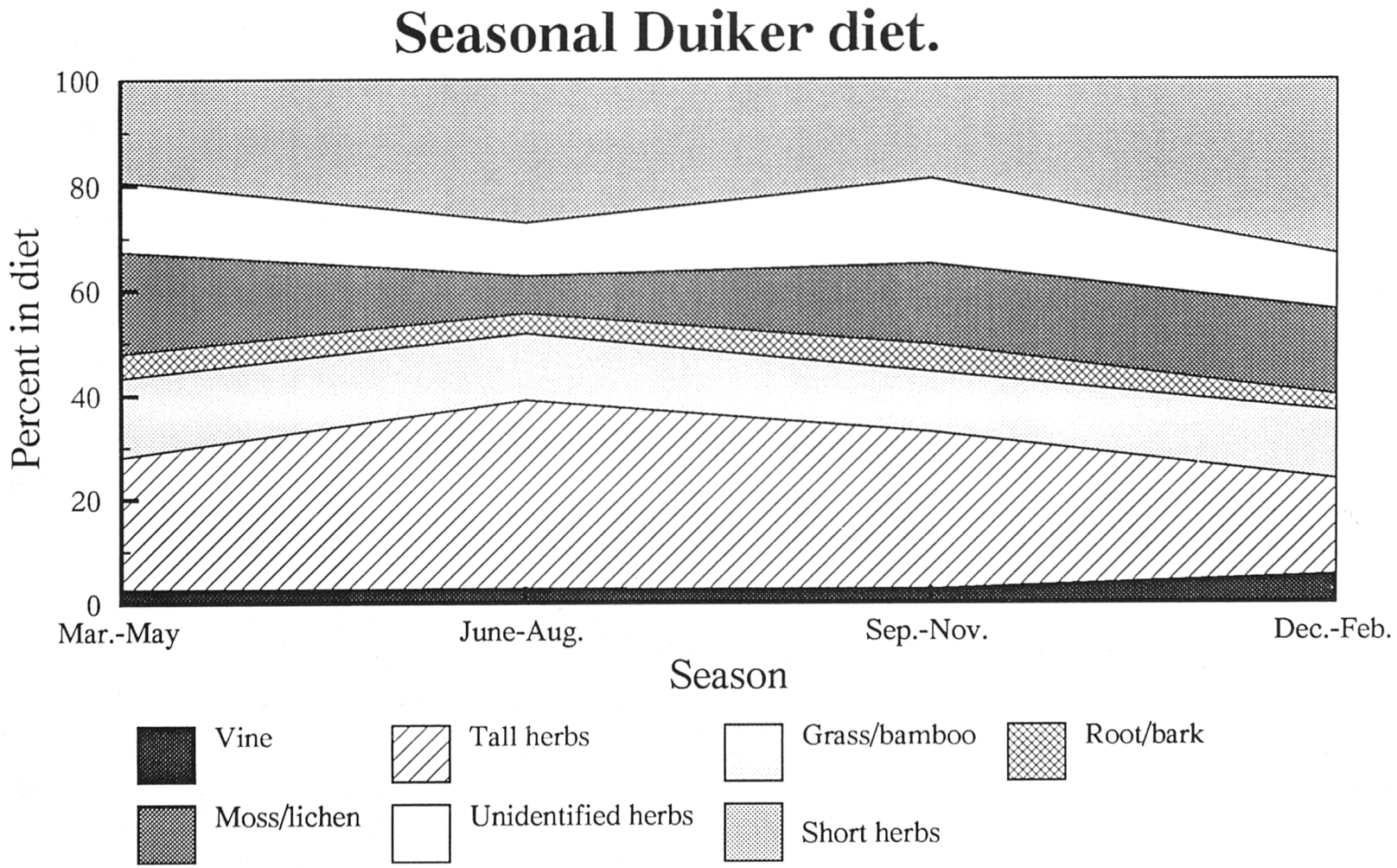


Figure 4.7 The seasonal variation in the diet of the duikers in the study area in terms of the proportional biomass ingested of the main plant types. Figures are based on the values obtained from microhistological analysis for each season.

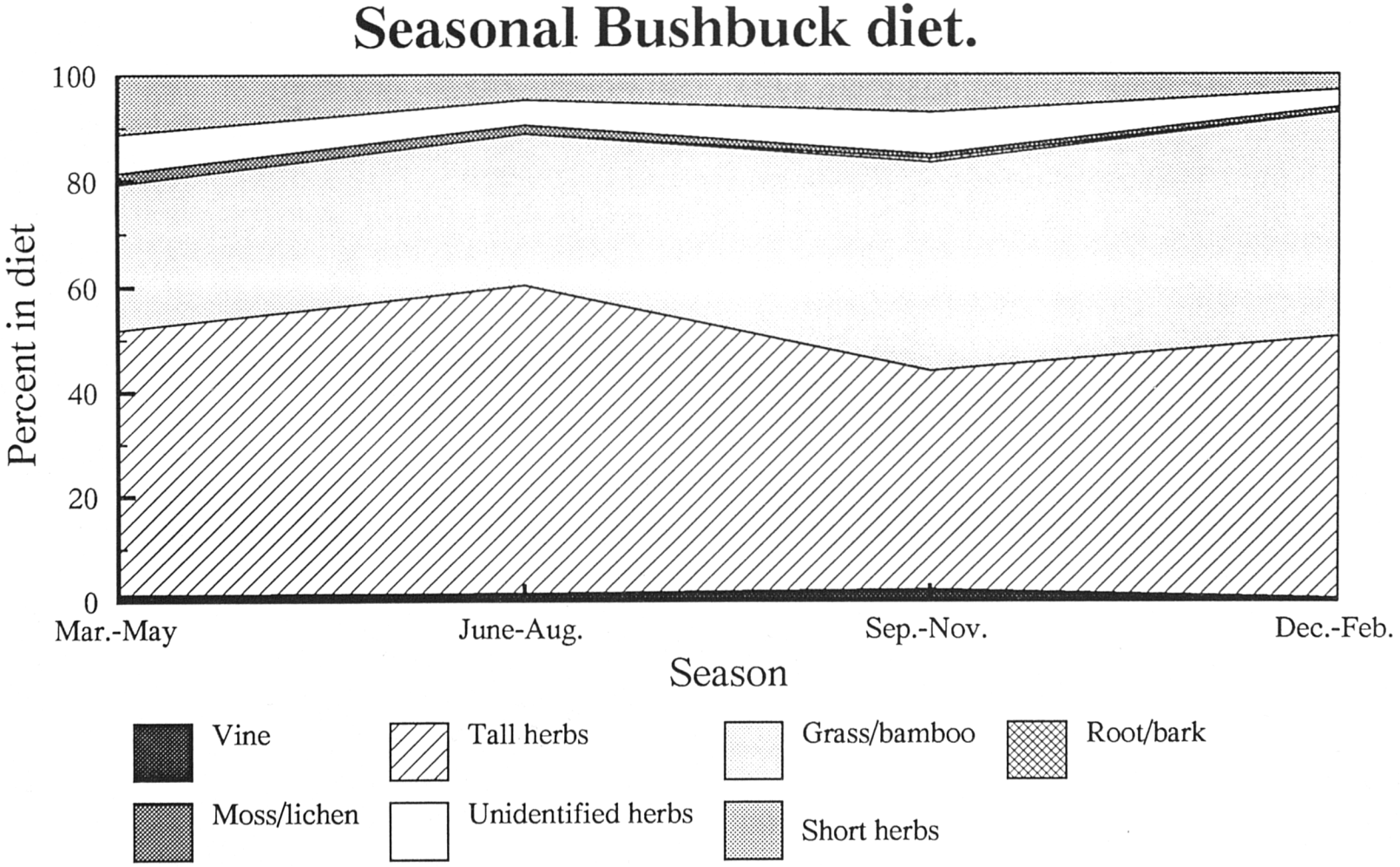


Figure 4.8 The seasonal variation in the diet of the bushbuck in the study area in terms of the proportional biomass ingested of the main plant types. Figures are based on the values obtained from microhistological analysis for each season.

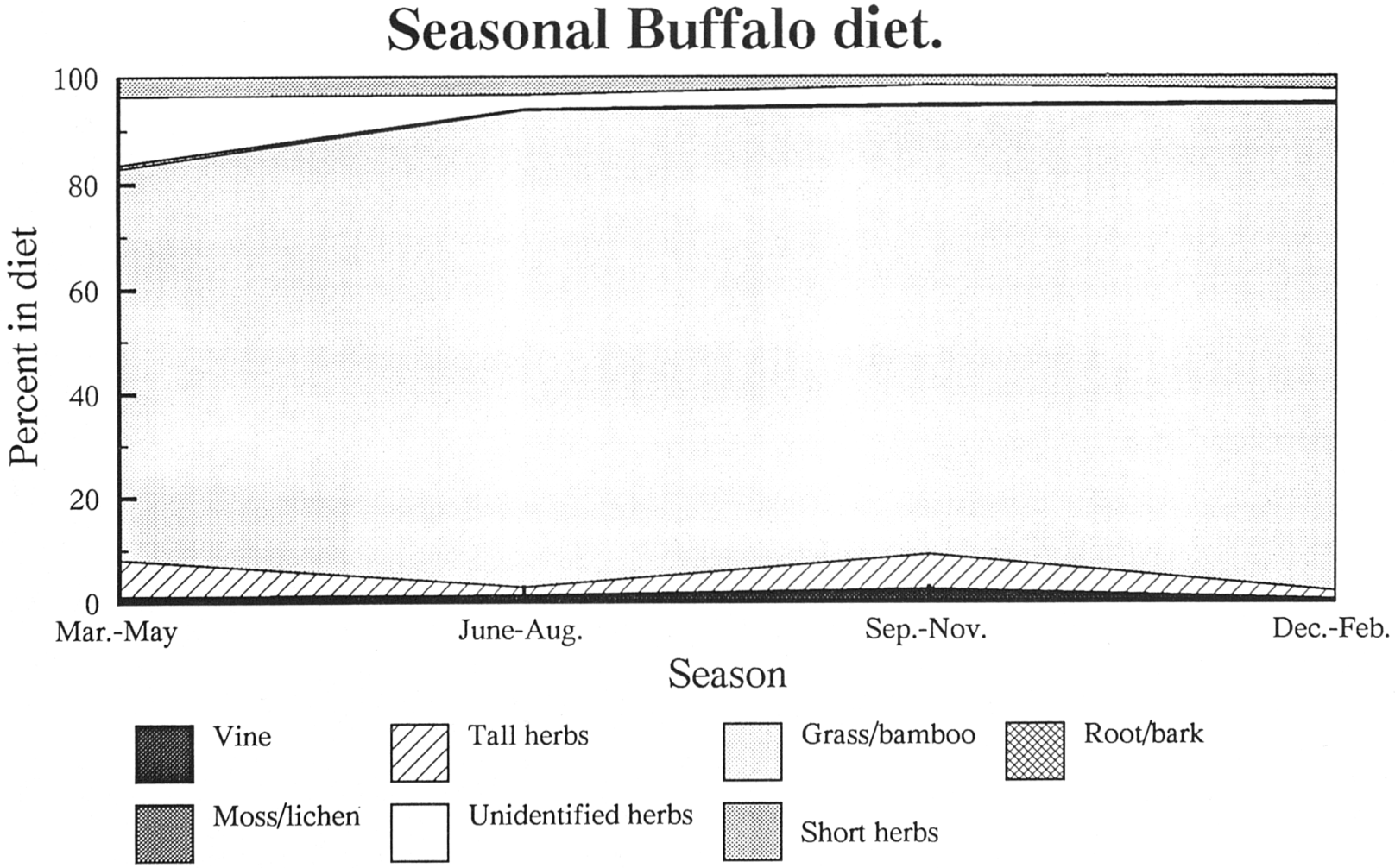


Figure 4.9 The seasonal variation in the diet of the buffalo in the study area in terms of the proportional biomass ingested of the main plant types. Figures are based on the values obtained from microhistological analysis for each season.

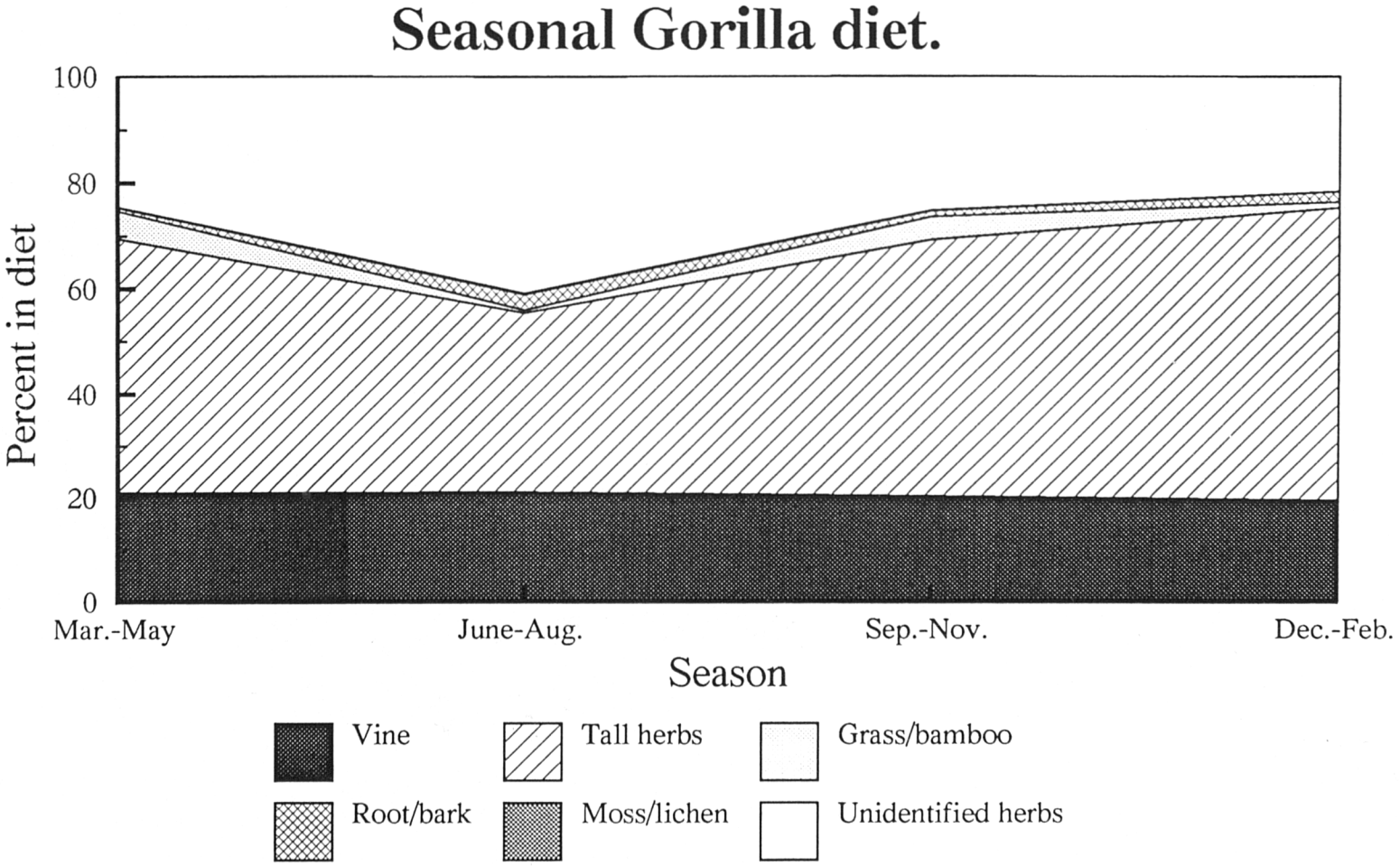


Figure 4.10 The seasonal variation in the diet of the gorillas in the study area in terms of the proportional biomass ingested of the main plant types. Figures are based on the values obtained from microhistological analysis for each season.

4.3.3 Preference

Both Manly's alpha (Chesson 1983, Krebs 1989) and Ivlev's measure of electivity (Krebs 1989) were used to measure dietary preferences. These are given in Tables 4.4 to 4.8. A criticism of Ivlev's measure of preference (electivity) is that the value depends not only upon consumer behaviour but also on the amount of each food type present. The value of Manly's alpha does not change with food density unless consumer behaviour changes (Chesson 1983) and hence it is considered a more reasonable measure (Krebs 1989).

Using either measure it can be seen that the caecal fermenters were more selective, showing a preference for fewer plant species and an avoidance for more plant species than the ruminants. This may be because most plant species available to the gorillas and elephant are too small in size to be eaten and hence they may not be avoiding them but simply do not sample them.

4.3.4 Feeding height

The distribution of feeding heights is shown in Figure 4.11. There is no measure for the gorillas as most of the time they will break off a plant at ground level and strip it of leaves or simply run their hands up the stem stripping the leaves off, thereby making it difficult to assign a feeding height. There was some degree of separation in the heights at which the herbivores were feeding, although since elephant and buffalo were measured from trail signs some of the lower heights may have been missed. Not every grass species cropped by the buffalo was measured as some could not be distinguished from the surrounding vegetation, particularly where the sward was kept short by constant cropping.

Table 4.4 The preference by duiker for different food items or groups of food species using Ivlev's measure of electivity and Manly's alpha. Where Manly's alpha shows a selection by these animals greater than expected it is marked by an asterisk. Anything greater than zero shows a preference under the electivity measure.

Plant species	Electivity	Manly's alpha	
Galium	0.576	0.011	
Laportea	-0.970	0.000	
Carduus	-0.093	0.002	
Impatiens	0.858	0.038	*
Solenostemon	-0.470	0.001	
C.simensis	-0.803	0.000	
C.bequaertii	-1.000	0.000	
C.erythrorr.	-0.765	0.000	
Mariscus/Panicum	-1.000	0.000	
Arundinaria	-1.000	0.000	
Agrostis/F.Schimper.	0.810	0.028	
F.engleri	0.150	0.004	
Crassoceph.	-1.000	0.000	
Hypericum	0.722	0.018	
Plectranthus	-0.751	0.000	
Rubus	0.159	0.004	
Selaginella/Moss	0.161	0.004	
Pilea	0.790	0.025	
Cerastium/Stellaria	0.906	0.059	*
Luzula	0.146	0.004	
Alchemilla/Ranunculus	0.657	0.014	
P.communis/Oxalis	0.768	0.022	
Gynura/Stachys	0.437	0.007	
Geranium/Droquetia	0.866	0.041	*
Hydroctyle/Hyp.peplid.	-1.000	0.000	
Mentha	0.934	0.086	*
P.linderi/Oenanthe	-0.444	0.001	
Viola/Tylophorops.	0.884	0.047	*
Alch.john./Helichrysum	0.264	0.005	
Lob.giberr./Echinops	-1.000	0.000	
Polygonum/P.kerstenii	-0.004	0.003	
Plantago/Trifolium	0.990	0.576	*
Stephania/Urtica/Girar.	-1.000	0.000	
Stems:			
P.linderi	-1.000	0.000	
Carduus	-1.000	0.000	
Laportea	-1.000	0.000	
No. preferred	18	6	

Electivity = $\frac{r_i - n_i}{r_i + n_i}$ **Manly's alpha**$_i$ = $\frac{r_i}{n_i \Sigma (r_j/n_j)}$

where r_i, r_j = proportion of prey type *i* or *j* in the diet
n_i, n_j = proportion of prey type *i/j* in the environment
j = 1,2,3,...,m (where m = total number of prey types)

Table 4.5 The preference by bushbuck for different food items or groups of food species using Ivlev's measure of electivity and Manly's alpha. Where Manly's alpha shows a selection by these animals greater than expected it is marked by an asterisk. Anything greater than zero shows a preference under the electivity measure.

Plant species	Electivity	Manly's alpha	
Galium spp.	0.054	0.005	
Laportea alatipes	0.095	0.006	
Carduus nyassanus	-0.318	0.003	
Impatiens spp.	0.802	0.044	*
Solenostemon sylvaticum	0.420	0.012	
C.simensis	0.018	0.005	
C.bequaertii	0.209	0.007	
C.erythrorhiza	-0.681	0.001	
Mariscus/Panicum	0.768	0.037	*
Arundinaria alpina	0.952	0.197	*
Agrostis/F. schimperiana	0.864	0.067	*
F.engleri	0.069	0.006	
Crassocephalum ducis-aprutii	-0.762	0.001	
Hypericum revolutum	0.788	0.041	*
Plectranthus sylvestris	-0.926	0.000	
Rubus spp.	0.900	0.093	*
Selaginella/Moss	0.007	0.005	
Pilea rivularis	-1.000	0.000	
Cerastium/Stellaria	0.551	0.017	
Luzula spp.	0.421	0.012	
Alchemilla/Ranunculus	0.504	0.015	
P. communis/Oxalis	-1.000	0.000	
Gynura/Stachys	-0.058	0.004	
Geranium/Droquetia	0.116	0.006	
Hydroctyle/H. peplidifolium	-0.814	0.000	
Mentha aquatica	0.116	0.006	
P. linderi/Oenanthe	0.080	0.006	
Viola/Tylophoropsis	0.168	0.007	
A. johnstonii/Helichrysum	-0.622	0.001	
L. giberroa/Echinops	-1.000	0.000	
Polygonum/P. kerstenii	-0.425	0.002	
Plantago/Trifolium	0.976	0.394	*
Stephania/Urtica/Girardinia	-1.000	0.000	
Stems:			
P. linderi	-1.000	0.000	
Carduus nyassanus	-1.000	0.000	
Laportea alatipes	-1.000	0.000	
No. preferred	21	7	

Electivity = $\frac{r_i - n_i}{r_i + n_i}$ **Manly's alpha**$_i$ = $\frac{r_i}{n_i} \frac{1}{\Sigma(r_j/n_j)}$

where r_i, r_j = proportion of prey type *i* or *j* in the diet
n_i, n_j = proportion of prey type *i/j* in the environment
j = 1,2,3,...,m (where m = total number of prey types)

Table 4.6 The preference by buffalo for different food items or groups of food species using Ivlev's measure of electivity and Manly's alpha. Where Manly's alpha shows a selection by these animals greater than expected it is marked by an asterisk. Anything greater than zero shows a preference under the electivity measure.

Plant species	Electivity	Manly's alpha	
Galium spp.	0.173	0.009	
Laportea alatipes	-1.000	0.000	
Carduus nyassanus	-1.000	0.000	
Impatiens spp.	0.399	0.015	
Solenostemon sylvaticum	-1.000	0.000	
C.simensis	0.647	0.030	*
C.bequaertii	0.854	0.083	*
C.erythrorhiza	0.659	0.032	*
Mariscus/Panicum	-0.058	0.006	
Arundinaria alpina	0.975	0.522	*
Agrostis/F. schimperiana	0.815	0.064	*
F. engleri	0.688	0.035	*
Crassocephalum ducis-aprutii	-0.898	0.000	
Hypericum revolutum	-1.000	0.000	
Plectranthus sylvestris	-1.000	0.000	
Rubus spp.	-1.000	0.000	
Selaginella/Moss	-0.686	0.001	
Pilea rivularis	-1.000	0.000	
Cerastium/Stellaria	0.407	0.015	
Luzula spp.	-0.104	0.005	
Alchemilla/Ranunculus	-0.636	0.001	
P. communis/Oxalis	-1.000	0.000	
Gynura/Stachys	-1.000	0.000	
Geranium/Droquetia	-1.000	0.000	
Hydroctyle/H. peplidifolium	-1.000	0.000	
Mentha aquatica	0.112	0.008	
P. linderi/Oenanthe	0.399	0.015	
Viola/Tylophoropsis	0.163	0.009	
A. johnstonii/Helichrysum	-0.733	0.001	
L. giberroa/Echinops	-1.000	0.000	
Polygonum/P. kerstenii	-1.000	0.000	
Plantago/Trifolium	0.905	0.130	*
Stephania/Urtica/Girardinia	-1.000	0.000	
Stems:			
P. linderi	0.425	0.016	
Carduus nyassanus	-1.000	0.000	
Laportea alatipes	-1.000	0.000	
No. preferred	14	7	

Electivity = $\frac{r_i - n_i}{r_i + n_i}$ Manly's alpha$_i$ = $\frac{r_i}{n_i} \frac{1}{\Sigma(r_j/n_j)}$

where r_i, r_j = proportion of prey type *i* or *j* in the diet
n_i, n_j = proportion of prey type *i*/*j* in the environment
j = 1,2,3,...,m (where m = total number of prey types)

Table 4.7 The preference by gorillas for different food items or groups of food species using Ivlev's measure of electivity and Manly's alpha. Where Manly's alpha shows a selection by these animals greater than expected it is marked by an asterisk. Anything greater than zero shows a preference under the electivity measure.

Plant species	Electivity	Manly's alpha	
Galium spp.	0.882	0.081	*
Laportea alatipes	0.295	0.009	
Carduus nyassanus	0.589	0.020	
Impatiens spp.	-0.903	0.000	
Solenostemon sylvaticum	-1.000	0.000	
C.simensis	-0.788	0.001	
C.bequaertii	-0.875	0.000	
C.erythrorhiza	-1.000	0.000	
Mariscus/Panicum	-1.000	0.000	
Arundinaria alpina	0.986	0.724	*
Agrostis/F. schimperiana	-1.000	0.000	
F.engleri	-1.000	0.000	
Crassocephalum ducis-aprutii	-1.000	0.000	
Hypericum revolutum	-1.000	0.000	
Plectranthus sylvestris	-1.000	0.000	
Rubus spp.	0.888	0.086	*
Selaginella/Moss	-0.928	0.000	
Pilea rivularis	-0.796	0.001	
Cerastium/Stellaria	-0.580	0.001	
Luzula spp.	-1.000	0.000	
Alchemilla/Ranunculus	-1.000	0.000	
P. communis/Oxalis	-1.000	0.000	
Gynura/Stachys	-0.542	0.002	
Geranium/Droquetia	0.582	0.019	
Hydroctyle/H. peplidifolium	-0.902	0.000	
Mentha aquatica	-1.000	0.000	
P. linderi/Oenanthe	-1.000	0.000	
Viola/Tylophoropsis	-0.562	0.001	
A. johnstonii/Helichrysum	-1.000	0.000	
L. giberroa/Echinops	-1.000	0.000	
Polygonum/P. kerstenii	-1.000	0.000	
Plantago/Trifolium	-1.000	0.000	
Stephania/Urtica/Girardinia	-1.000	0.000	
Stems:			
P. linderi	0.762	0.038	*
Carduus nyassanus	0.460	0.014	
Laportea alatipes	-0.557	0.001	
No. preferred	8	4	

Electivity = $\frac{r_i - n_i}{r_i + n_i}$ **Manly's alpha**$_i$ = $\frac{r_i}{n_i \sum (r_j/n_j)} \frac{1}{}$

where r_i, r_j = proportion of prey type *i* or *j* in the diet
n_i, n_j = proportion of prey type *i*/*j* in the environment
j = 1,2,3,...,m (where m = total number of prey types)

Table 4.8 The preference by elephant for different food items or groups of food species using Ivlev's measure of electivity and Manly's alpha. Where Manly's alpha shows a selection by these animals greater than expected it is marked by an asterisk. Anything greater than zero shows a preference under the electivity measure.

Plant species	Electivity	Manly's alpha	
Galium spp.	-0.112	0.002	
Laportea alatipes	0.169	0.003	
Carduus nyassanus	0.171	0.003	
Impatiens spp.	-1.000	0.000	
Solenostemon sylvaticum	-0.919	0.000	
C.simensis	-0.209	0.002	
C.bequaertii	0.792	0.020	
C.erythrorhiza	-1.000	0.000	
Mariscus/Panicum	-1.000	0.000	
Arundinaria alpina	0.995	0.925	*
Agrostis/F. schimperiana	-1.000	0.000	
F.engleri	-1.000	0.000	
Crassocephalum ducis-aprutii	-0.982	0.000	
Hypericum revolutum	0.257	0.004	
Plectranthus sylvestris	-1.000	0.000	
Rubus spp.	0.544	0.008	
Selaginella/Moss	-1.000	0.000	
Pilea rivularis	-1.000	0.000	
Cerastium/Stellaria	-1.000	0.000	
Luzula spp.	-1.000	0.000	
Alchemilla/Ranunculus	-1.000	0.000	
P. communis/Oxalis	-1.000	0.000	
Gynura/Stachys	-0.540	0.001	
Geranium/Droquetia	0.119	0.003	
Hydroctyle/H. peplidifolium	-1.000	0.000	
Mentha aquatica	-1.000	0.000	
P. linderi/Oenanthe	-0.854	0.000	
Viola/Tylophorops.	-0.560	0.001	
A. johnstonii/Helichrysum	-1.000	0.000	
L. giberroa/Echinops	-0.387	0.001	
Polygonum/P. kerstenii	-1.000	0.000	
Plantago/Trifolium	-1.000	0.000	
Stephania/Urtica/Girardinia	0.348	0.005	
Stems:			
P. linderi	-0.308	0.001	
Carduus nyassanus	0.778	0.019	
Laportea alatipes	0.058	0.003	
No. preferred	**10**	**1**	

Electivity = $\frac{r_i - n_i}{r_i + n_i}$ **Manly's alpha**$_i$ = $\frac{r_i}{n_i \frac{1}{\Sigma(r_j/n_j)}}$

where r_i, r_j = proportion of prey type *i* or *j* in the diet
n_i, n_j = proportion of prey type *i/j* in the environment
j = 1,2,3,...,m (where m = total number of prey types)

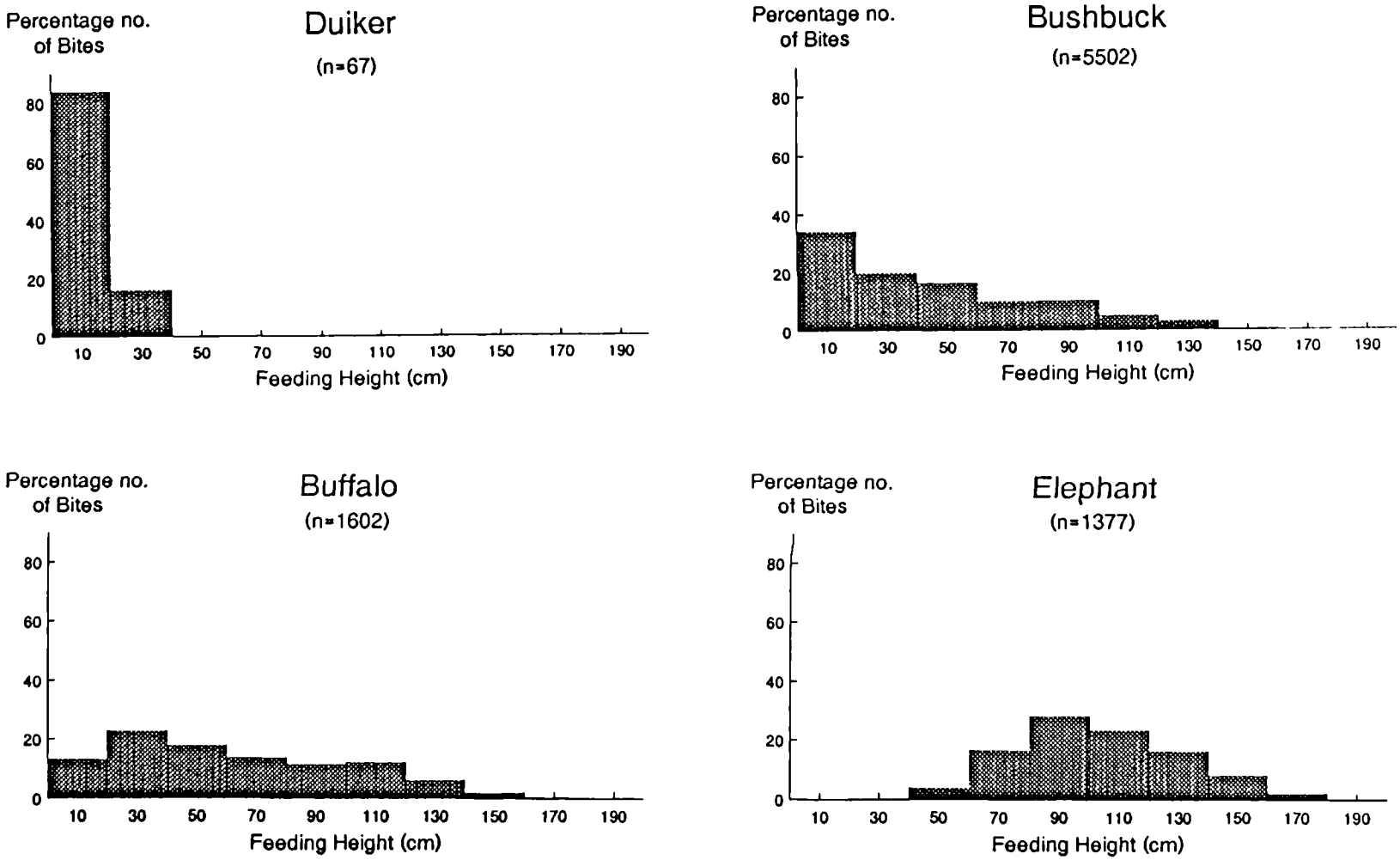


Figure 4.11 The distribution of heights at which the herbivores feed when in a habitat with a wide range of possible feeding heights. Bushbuck and duiker data were collected by observing the animals whilst elephant and buffalo data came from measuring the height of vegetation that they had browsed. Gorillas run their hands up tall plants stripping the leaves and hence cannot be said to feed at any particular height.

4.3.5 Nutrient content of the diet

The nutrient content of the major plant species is given in Table 4.9. Phosphorus levels were only obtained for a few species because of equipment failure and so some figures have been taken from Watts (1983). There was good agreement between the results given here for the other nutrients and digestibility and those given by Watts (1983) for the gorilla food plant species. There did not appear to be much difference in the nutrient content, ash content or digestibility between the wet and dry seasons. Only zinc varied by much but there was no consistent pattern between seasons. Protein content was calculated as 6.25xNitrogen content (Crampton & Harris 1969). Some levels of protein seem particularly high (for example *Urtica massaica* has a level of 39.4%) and these figures were checked by the Welsh Plant Breeding station, which regularly analyses nitrogen concentrations. Their figures over the whole spectrum of variation were similar.

Dietary protein calculated from the protein levels for each plant species multiplied by their proportion in the diet are given in Table 4.10. Mean faecal protein levels are also given for the sample of dried faeces collected. The seasonal variation in faecal protein levels is shown for the four herbivores found in the study area throughout the year in Figure 4.12. Table 4.10 also gives a corrected estimate of dietary protein intake calculated from the faecal protein levels using equations given in Arman, Hopcraft & McDonald (1975). Initially the equation given by Sinclair (1977) was used, but this gave highly elevated results for all species. This was probably because it was calculated for a low protein diet. The non-ruminant equation used here was based on data collected for a diet of grass, which might explain why the corrected level for the gorilla and elephant are lower than the dietary intake. On the other hand the dietary protein intake does not include the protein content of all stems eaten because figures were not obtained for these. Watts (1983) calculated the protein

Table 4.9 The digestibility (CDIG), ash and nutrient content of the leaves of each of the main food-plant species consumed by each herbivore species. Some major dietary items were measured during different seasons as indicated. All values are given in percentage dry mass unless indicated otherwise.

Plant species	CDIG	Protein	P	K	Ca	Mg	Zn (ug/g)	Cu (ug/g)	Ash
Vine:									
Galium	76	19.5	0.50	3.46	1.47	0.39	98.3	3.8	13.4
Gynura	65	28.9		6.36	1.03	0.37	33.0	17.5	31.3
Tall herbs:									
Laportea (apr)	64	28.3	0.33	3.37	2.28	0.64	59.8	10.2	15.3
Laportea (jun)	64	27.4		3.04	2.40	0.65	59.5	9.0	14.8
Urtica	81	39.4	0.57	4.20	3.88	0.71	82.3	12.8	23.0
Girardinia	69	24.1		2.96	3.26	0.85	86.8	9.6	21.3
Carduus (apr)	62	28.5	0.33	4.22	1.96	0.35	251.0	25.9	13.5
Carduus (jun)	65	31.4		4.82	1.78	0.36	78.0	18.6	14.4
Echinops	61	19.6		4.42	0.83	0.29	24.9	13.5	11.1
Impatiens	62	30.4	0.40	4.08	1.80	0.60	92.3	17.1	13.9
Solenostemon	35	27.3	0.41	3.27	1.43	0.67	88.0	21.5	14.5
Plectranthus	51	27.4		3.18	0.91	0.47	153.5	14.2	11.4
Crassocephalum	54	32.8		5.13	0.81	0.34	111.2	19.4	14.4
P. linderi	80	36.9		4.66	0.84	0.27	96.7	9.3	11.6
Oenanthe	67	33.6		5.40	0.71	0.39	25.7	16.6	21.4
Stachys	56	21.2		3.04	1.11	0.57	31.5	13.7	9.6
Grasses:									
C. simensis (feb)	30	20.9	0.73	2.23	0.33	0.29	138.5	9.8	9.3
C. simensis (apr)	29	21.9		2.49	0.26	0.24	65.9	11.3	10.2
C. bequaertii	26	16.3	0.13	1.69	0.27	0.15	93.5	11.4	5.6
C. erythroriza	30	18.9		2.03	0.28	0.25	84.3	10.1	7.9
Mariscus	47	20.3		3.23	0.76	0.51	44.2	9.4	10.1
Arundinaria	30	20.8	0.18	1.44	0.32	0.16	36.7	8.4	11.6
Agrostis	43	13.6		1.82	0.23	0.24	32.6	8.9	6.2
Poa annua	42	15.3		3.71	0.38	0.24	164.7	12.0	12.1
F. schimperana (feb)	32	14.5	0.26	1.92	0.67	0.23	68.8	8.6	9.6
F. schimperana (apr)	39	15.9		1.99	0.55	0.22	125.9	7.7	9.2
F. engleri	47	28.0	0.30	4.01	0.23	0.23	184.2	10.4	10.8
Woody lvs:									
Lobelia giberroa	76	26.1		3.35	0.86	0.49	436.6	8.5	10.4
H. revolutum	29	29.1		1.34	0.33	0.23	50.2	14.1	5.0
Hagenia (green)	49	21.8		1.26	0.54	0.25	28.7	8.6	4.9
Hagenia (dead)	29	6.6		0.47	0.82	0.20	11.0	5.6	4.3
S. aculeastrum	69	29.5		2.40	1.26	0.30	36.1	17.3	7.9

Table 4.9 (continued)

Plant species	CDIG	Protein	P	K	Ca	Mg	Zn (ug/g)	Cu (ug/g)	Ash
Small herbs:									
Pilea	56	21.3		1.89	3.78	0.90	33.4	11.5	18.2
Cerastium (feb)	48	21.5		6.40	0.80	0.39	223.3	5.4	16.0
Cerastium (apr)	51	24.3		6.46	0.72	0.40	462.0	4.2	15.3
Cardamine obliqua	80	26.2		4.47	1.30	0.57	339.7	4.7	14.0
Rumex bequaertii	67	31.4		6.08	0.43	0.46	104.5	9.0	13.3
Stellaria	60	21.6		6.67	1.05	0.49	142.0	6.8	16.8
Ranunculus bequaertii	79	21.4		3.05	0.92	0.34	190.8	17.6	10.1
R. multifidus	76	23.9		3.58	0.87	0.36	88.9	19.0	9.7
P. communis	52	25.7		3.30	0.92	0.44	151.5	8.5	10.1
Geranium	77	24.8		2.37	1.46	0.30	192.6	6.2	8.6
Hydroctyle	66	21.6		3.98	1.91	0.45	328.2	21.1	14.8
Mentha	58	26.8		2.73	1.79	1.22	202.4	14.6	11.1
Viola	70	24.5		3.21	1.61	0.99	599.9	12.1	13.0
Helichrysum globosum	55	18.0		4.81	0.80	0.42	84.2	11.7	11.8
Polygonum	70	31.8		3.21	1.09	0.72	200.5	11.2	11.1
Plantago	72	24.1		3.95	2.44	0.44	316.2	25.7	14.8
Moss:									
Selaginella	50	22.0		3.01	0.43	0.39	214.3	8.5	10.3
Other:									
Usnea Lichen	29	9.6	0.05	0.28	0.26	0.09	111.4	1.7	1.7
Hypericum bark	38	5.3	0.03	0.60	0.39	0.11	70.8	8.4	2.4

Table 4.10 The percentage protein in the diet and faeces of each herbivore species. Dietary nitrogen is also calculated, correcting faecal nitrogen values using the equations given below.

Protein = 6.25 x Percentage nitrogen.

	Dietary protein	Faecal protein	Corrected Faecal protein
Duiker	21.0	25.6	20.5
Bushbuck	23.5	24.4	19.8
Buffalo	19.2	18.9	16.6
Gorilla	19.3	24.1	13.3
Elephant	13.4	11.1	8.1

Correction equations to estimate dietary nitrogen (DN) from faecal nitrogen (FN):

Ruminants $_{(Legumes)}$: DN = 0.592xFN + 8.6
Ruminants $_{(grass)}$: DN = 0.433xFN + 8.4
Non-Ruminants DN = 0.4xFN + 5.9

DN & FN measured in g/kg.
(Arman, Hopcraft & McDonald 1975)

Faecal protein levels.

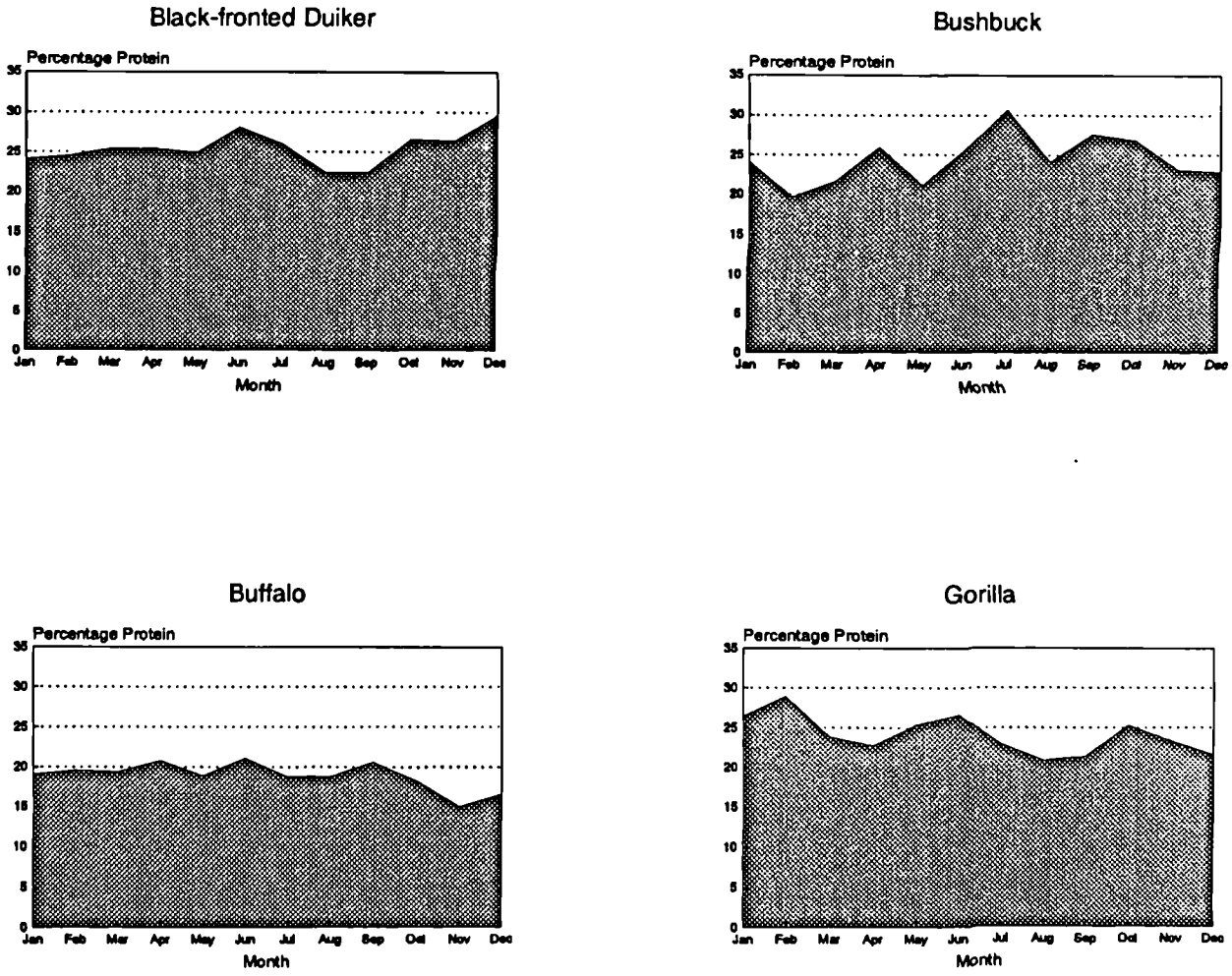


Figure 4.12 Faecal protein levels obtained from faecal material collected monthly during 1989 for each of the herbivore species that were in the study area during this time. Faecal protein is calculated as 6.25 x Faecal nitrogen.

intake of the gorillas as 13.9% which is closer to the corrected faecal measure. The elephant faeces were collected from the bamboo in November (between Bisoke and Sabinyo) when they were eating bamboo shoots. A similar measure was obtained separately for the gorilla group using the Bamboo zone and the other groups at the same time which indicates that the animals in the bamboo have a lower protein intake than elsewhere (17.6% compared with 23.4% faecal content).

A multiple linear regression model was used to relate the nutrients measured in the plants to the actual diets of each of the animals. A stepwise procedure of selection was used with a confidence level of F = 0.05 for inclusion into the model. Only buffalo showed any significant correlation and this was a negative correlation with digestibility ($F=9.94$, d.f.=31, $P<0.05$). However, even this correlation is fairly weak ($R_{adj}= 0.22$). If the availability of plants was included in the model with the nutrients then both the elephant and gorillas showed a poor but significant correlation with availability (Gorilla: $F=4.74$, d.f.=31, $P<0.05$, $R_{adj}=0.10$; Elephant: $F=5.79$, d.f.=31, $P<0.05$, $R_{adj}=0.13$). Otherwise none of the other nutrients passed the 5% inclusion level and therefore were not being selected by the herbivores. If only those plants eaten by the animal were used in the model rather than all the plants available, then duiker, bushbuck and elephant showed no correlation with any of the nutrients, ash content, digestibility or availability. Buffalo showed a slightly stronger negative correlation with digestibility ($F=10.61$, d.f.=17, $P<0.01$, $R_{adj}=0.35$) and gorillas showed a positive correlation with digestibility and with availability (the latter being a stronger factor) ($F=13.15$, d.f.=10, $P<0.01$, $R_{adj}=0.67$).

4.4 Discussion

4.4.1 Diet

Given the inaccuracies inherent in faecal analysis (Gill *et al.* 1983) it is prudent to be cautious about results generated by this method. The species of plant found in the diet are not unreasonable given the plants these animals have been seen to eat (Watts 1983, Tangishaka 1988, pers. obs.). The proportional intake of the gorillas did differ from that recorded by Watts (1983, corrected to dry mass using water content values) from visual observation, however both techniques identified *Galium, Laportea alatipes* and *Carduus nyassanus* as forming the major leaf items in the diet. It is also ten years since his study and changes could have occurred in the diets of the gorillas since then.

The figure of 14.8% for lichen intake by the duiker may have been higher than the actual intake because the area of identifiable lichen could not easily be assigned a mass. However a low mass relative to the plant species was used and this should mean that this is a conservative estimate. Duiker were observed to feed on the lichen *Usnea* wherever possible, often standing on their hind legs to reach it. This is surprising given the low digestibility and nutrient content relative to the other plant species. Reindeer in Norway seem to select the lichens because they are rich in sugars (N.Tyler pers. comm.). In lowland tropical rainforest the black-fronted duikers have been found to be mainly frugivorous, fruit forming about 70% of the diet (Dubost 1984). There is little fruit in the Birungas, but since fruit is rich in sugar it may be that these animals require the lichen to supplement their sugar levels. Similarly, the gorillas in western Africa also have a high quantity of fruit in their diet (Tutin & Fernandez 1985, Rogers *et al.* 1990).

This shows how flexible the diets of animal species can be. Studies such as this are over a short "window in time" and the diet measured at this time is likely to change. Walker (1979) suggested that there is an "even pressure of use over all components of the vegetation" even if the use by a particular species varies. Therefore animals will adapt their diets to some extent to exploit whatever they can as it becomes available. Prins & Douglas-Hamilton (1990) showed that this was true for Lake Manyara National Park. The pressure on the vegetation here has remained fairly constant between 1959 and 1984, despite large fluctuations in the numbers of individual species. They concluded that the pressure on the vegetation has varied much less than the composition of the herbivore assemblage.

4.4.2 Preference

A.Vedder (pers. comm.) found that the preference for plant species can change depending on the scale at which it is studied. For instance, at the scale of "home range" she found the preference for *Galium* by mountain gorillas to be relatively high. However, at the scale of choice "within arms reach" the preference dropped compared to some other plants. This is because the vegetation is not uniform but is patchy throughout the Birungas (Chapter 2), so that the gorillas are selecting feeding areas which have a higher biomass of *Galium* than the mean value and because of this the preference level drops. In this study it was only possible to calculate preference at the largest scale using the vegetation availability throughout the study area. This tends to increase the preference for relatively rare items such as *Arundinaria* (bamboo) leaves, which may not be preferred when the animal is actually in the bamboo. None of the preferences found are unexpected, given what was seen when observing the animals or their trails, and this further confirms that the faecal analysis is fairly accurate.

4.4.3 Nutrition

Grace (1983) gave the following levels of minerals in herbage as easily sufficient to maintain body condition in cattle and sheep:

1. Phosphorus: 0.25-0.3%
2. Potassium: 0.2-0.6%
3. Calcium: 0.29-0.44%
4. Magnesium: 0.12-0.19%
5. Zinc: 17-25 ug g^{-1}
6. Copper: 5-6 ug g^{-1}

Most species of plant tested have levels well over these values. Some of the grass species are low in calcium, magnesium and phosphorus and a few small herbs and *Galium* are low in copper, however in general there are adequate levels of these nutrients for the herbivores. Nitrogen or protein has been shown to limit the populations of buffalo in East Africa (Sinclair 1977) and has been considered by some to be the most critical parameter limiting food quality for herbivores (White 1978). Other studies however, have found digestible energy to be a more critical parameter (Owen-Smith & Cooper 1989) The minimum requirement for protein in the diet of cattle or buffalo is about 7% (Prins 1987) and most ruminants studied are around 7-10% (Crampton & Harris 1969, Wallmo *et al.* 1977, Carl & Brown 1985). Lactating females will require higher levels of protein, as will young animals (Sinclair 1977, Wallmo *et al* 1977). Knowledge about non-ruminant requirements for protein are less clear. Pigs are generally given higher protein levels in their feed (Crampton & Harris 1969), whereas horses can survive on about 6% protein (Crampton & Harris 1969, Van Soest 1982). This may be because pigs tend to be omnivorous rather than herbivorous. From the faecal nitrogen analysis it can be seen that protein levels in the diet never fall below that required for maintenance and probably not below that required for pregnant females or young. Hobbs (1987)

pointed out that not all faecal nitrogen is necessarily due to protein since high tannin levels can also increase it. In the Birungas tannin levels are probably low and hence were unlikely to affect the analysis.

Since all the nutrients studied seem to be readily available to the herbivores, it is not surprising that the multiple regression of plant nutrients on intake levels did not identify any significant selection of nutrients by the herbivores. Watts (1983) used a similar analysis of food plants used by gorillas and showed a correlation between intake and digestibility, as was also found here. He also found a significant positive correlation with protein which was not found in this study because he included data on stem protein levels. Stems were not included in this study because stem material could not be identified in the faeces.

4.4.4 What limits the populations?

If these herbivores are not limited by nutrients and food is plentiful (see Chapter 2) what is limiting the size of the populations? In the case of the gorillas and elephant it may be that both populations are not at carrying capacity, since they are both slow to reproduce and hence population increases will be slow. The 1989 census results suggested that the gorilla population was still increasing. Since predation pressure was low in the study area, it could not be having a significant impact on the ungulate populations. Silica can be a limiting nutrient for any herbivore eating grasses; however, the ash content found in the grasses (Table 4.9) was not particularly high, implying that silica (like the other digestibility) inhibitors was low.

One possibility is that energy is a limiting factor. Owen-Smith (1982) suggested that in general browsers are energy limited rather than nutrient limited and Owen-Smith & Cooper (1989) showed that Kudu were energy limited despite the fact that protein and other nutrients were above that required to maintain body condition. It is likely

that the low temperatures found at around 3100m (Karisoke) were increasing the energy expenditure above a level that could be maintained by the herbivores' food supply. Ohsawa & Dunbar (1984) showed that Gelada baboons fail to produce as many offspring at higher altitudes in Ethiopia, despite the fact that food availability increased with altitude; they suggested that this was due to energy expenditure increasing. Certainly it was a subjective impression that there were many carcases of bushbuck fawns between March and August 1988, when temperatures were particularly low and rainfall was heavy (Hastings & Byers in press). On post-mortem examination most of these showed signs of respiratory stress consistent with pneumonia.

Duiker may be limited by behavioural factors rather than physical factors. Since the duiker appear to be territorial the availability of territories could limit any further increase in the population. Caughley & Krebs (1983) suggested that in general populations of mammals below 30kg in body mass are regulated by intrinsic factors such as behaviour rather than extrinsically.

Few buffalo carcases were found in the park; during the two year study only two were seen near Karisoke, despite the fact that skulls and bones can last a long time. Both of these animals had been killed by falling down a ravine. During the 1989 gorilla census people were asked to keep an eye out for signs of dead buffalo, but none were found throughout the whole park. However, during the two year study at least eight buffalo were killed outside the park whilst raiding crops. It is possible that this human predation is limiting the buffalo population. Another factor that could limit the buffalo population is the bulk density of the grass sward available to them. Chacon & Stobbs (1976) have shown that a standing crop of green leaves of 1000kg ha^{-1} can be considered as just adequate to maintain cattle. Below this level grazing time and intake drops. In the Birungas only the Meadows habitat type exceeds 1000kg ha^{-1} in terms of green leaf biomass. Therefore grasses would seem to be in short supply or at

least very patchily distributed. The question is why do the buffalo not use more of the abundant tall herbs? One possible reason is that the protein content is too great for their digestive system. Garrett (1970) showed that beef cattle fed diets containing 21% crude protein required 20% more feed to maintain equilibrium energy than did those animals on 12% crude protein. This is because there is an energetic expense involved in metabolising the excess amino acids. Such a phenomenon could also explain why the buffalo show a negative selection for digestibility in the multiple regression analysis.

In conclusion, it has been shown that the large herbivores are not limited by nutrient availability or by predators. Energy availability and requirements, however, could be important. Whilst it is unlikely that the energy content of plants will vary much between seasons, since there seems to be little seasonal difference in nutrient content, the requirements of the animals could certainly change between seasons. Whether energy is the limiting factor requires further study.

CHAPTER FIVE

HERBIVORE DAMAGE AND PLANT PRODUCTIVITY.

5.1 Introduction

Whilst herbivores will damage the Birunga ecosystem through grazing or browsing, this is not the only damage that is likely to occur. Trampling damage, particularly by the three largest herbivores, is very obvious after they have passed through an area and most of the ridges that border the ravines up Bisoke also have well worn paths that are maintained by the antelope (Schaller 1963, pers. obs.). Therefore as part of a study of the impact of these herbivores on the vegetation it was necessary to obtain a measure of this damage and of the plant productivity and rate of regeneration of the trampled vegetation.

Coe, Cumming & Phillipson (1976) showed that primary productivity in savanna ecosystems could be related to the amount of rainfall falling on an area up to about 1000mm yr^{-1}. Rainforests however receive much more than this with Karisoke receiving about 1,800mm yr^{-1} (Fossey 1983) and Leigh (1975) states that there is little evidence for a correlation between production and rainfall or evapotranspiration (as suggested by Rosenzweig 1968) in these ecosystems. Primary productivity is also far more variable than a relationship with rainfall might suggest. Whilst the mean productivity may be related to rainfall in the savannas, there are many other factors that can also increase or decrease productivity in an area. McNaughton (1985) showed that plants respond to increasing grazing pressure initially by increasing their production of above-ground plant tissue, but as grazing pressure becomes high this productivity decreases again. Simulated grazing by clipping grass showed that this increased the total green leaf weight, increased root nitrogen uptake and increased the

above-ground nitrogen levels (Ruess & McNaughton 1984). Similarly the addition of urea and faeces by herbivores to the land will increase nitrogen levels causing increased plant productivity in certain areas (Ruess & McNaughton 1984).

Watts (1987) found that tall herbaceous plants trampled in areas used by mountain gorillas as feeding sites also showed increased productivity compared to the surrounding vegetation, and that the stem density of plants in regeneration plots increased. Trampling damage is not new to the Birungas as cattle have been recorded as grazing in the park as long ago as the 1890's and Spinage (1972) noted that cattle were causing considerable damage to the forest in the early 1970s. It is likely therefore that plant species present in the park are resistant to this type of damage.

It can be seen therefore that herbivore damage can have both deleterious effects by removing available food and positive effects by increasing plant productivity and plant density. In this chapter I will look at some aspects of the plant dynamics.

5.2 Methodology

The productivity of the main plant species in the Birungas was measured in two ways. Since the height of the tall herbaceous plants such as nettles could be related to biomass (See Chapter 2), productivity of these plants was measured by marking 20 individuals of each species and of varying heights and measuring their heights at monthly intervals. For each species, individuals were chosen from more than one site to remove any bias due to soil nutrient status. Also, individuals were changed regularly so that effects due to the genetic variability within each individual plant could be reduced.

The productivity of the grasses and small herbs were measured by fencing off four plots, three of $4m^2$ and one of $3m^2$. The fencing excluded the large herbivores but allowed rodents and hyrax to enter the plot. After the initial fencing the plants were left to grow for three months after which the plots were clipped, sorted into species, dried and weighed to the nearest 0.1g. Total biomass inside the exclosure plot was compared with that outside by harvesting ten $0.1m^2$ plots outside each exclosure. Subsequent to this the plots were clipped at two month intervals for a year. In order to assess the increase in biomass since the previous clipping ten $0.1m^2$ plots were harvested after the final clipping to measure the biomass that remained in a plot after clipping had taken place. The four exclosure plots were placed in different types of vegetation to cover the main variation in the small herb types. Two were in areas of *Parochetus communis/Hydroctyle* spp., one exclosure was in a short grass meadow where the grass sward was only about 2-3cm deep and the last was in an area of long grass where only the growth of the small herbs and *Galium* was measured.

For both measures productivity was determined in terms of biomass increase per biomass of standing crop per day ($g\ g^{-1}\ d^{-1}$). In the case of the tall herbs standing crop biomass was simply the previous biomass. For the small herbs this value was taken as the proportion of the biomass that a plant species formed in the previous clipping multiplied by the mean biomass of plant material left in the exclosure after clipping had taken place. For the first cut this could not be measured because the initial proportions of the plants were not known, however an overall relative growth rate for the whole plot could be obtained. *Carex bequaertii* and *Festuca engleri* growth rates were measured by clipping clumps of these grasses at two monthly intervals at 40cm and 5cm respectively. At the final clipping the plant material remaining was also cut separately to obtain a measure of the standing crop.

A measure of the amount of trampling damage inflicted on the vegetation was obtained by walking transects (as for the faecal counts in Chapter 3) and measuring

the areas of flattened or regenerating vegetation crossing the three metre wide transect. Areas of damage were placed into one of four categories:

1. Elephant flattened vegetation
2. Gorilla flattened vegetation
3. Buffalo flattened vegetation
4. Path - no vegetation present because of constant use.

Flattening was recorded like this for each of the four seasons. The bulk of the flattening occurred in the Herbaceous, Saddle and Bamboo habitat types where the herbs were tall and dense. During the vegetation survey (Chapter 2) an assessment was made for each plot measured as to whether flattening damage would be noticeable and this provided a measure of the percentage of each habitat that would show flattening.

Regeneration of flattened areas was measured in the Herbaceous and Saddle/Bamboo regions after each species had visited an area. Initially in 1988 this was done by measuring the heights of plant species in $1m^2$ plots within the flattened regions. However it was found that this was very time consuming and did not provide enough samples. Therefore in late 1988 and 1989 it was decided to mark $1m^2$ plots in freshly flattened areas and visit them at monthly intervals, giving each plot a number on a scale from one to four (1=freshly flattened, 4=indistinguishable from the surrounding vegetation). This allowed many more plots to be measured in each habitat and reduced the variation that site specific differences in soil nutrient status could have on regeneration rates. It also allowed a test to be made between the regeneration rates of plots flattened in the wet or dry seasons.

5.3 Results

5.3.1. Productivity

The relative growth rate of all the tall herbs was found to vary depending on the age or stage of growth of the plant. The taller the plant the slower the relative growth rate was in general, although there is a lot of scatter in the measures (Figure 5.1). It is possible to fit an exponential curve through the points and the equations for each species are given in Appendix 5. When the growth rates are logged a straight line can be fitted through the points and tests between the straight lines produced by the wet and dry season growth rates were done using the formula given by Mead & Curnow (1983). This formula is as follows:

$$F=\frac{[RSS_T - (RSS_1 + RSS_2)]/2}{(RSS_1+RSS_2)/N}$$

RSS_T= Residual sum of squares of line fitted with combined data.

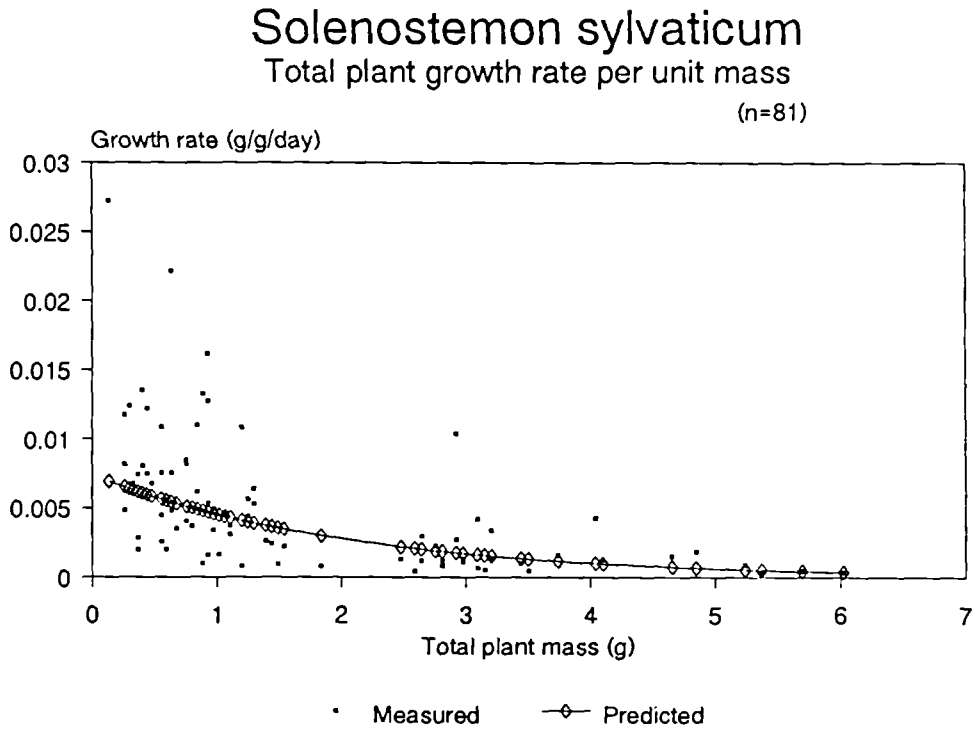
RSS_1= Residual sum of squares of first line.

RSS_2= Residual sum of squares of second line.

N = Sample size for combined data

These showed no significant difference between seasons for any species of plant.

The relative growth rates of the small herbs varied greatly for the exclosure plots and showed no obvious pattern or correlation with the climatic variables measured at Karisoke. This was partly because a low biomass of plant material at one clipping would elevate the estimate on the subsequent clipping. Therefore only the relative growth rates of the 'plant types' were calculated for each plot throughout the year (Figure 5.2). These showed a gradual decrease in productivity throughout the year.



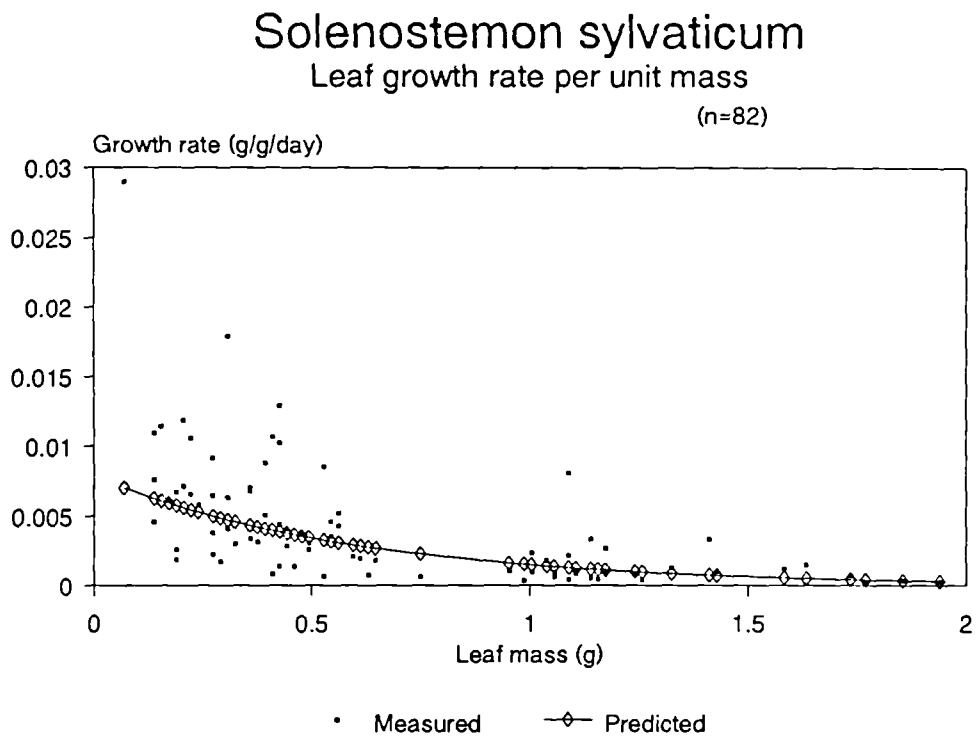


Figure 5.1 The growth rate of *Solenostemon sylvaticum* measured for the total mass of the plant and the leaf mass. An exponential curve ("predicted" line) was fitted through the data relating the relative growth rate of a plant to its mass.

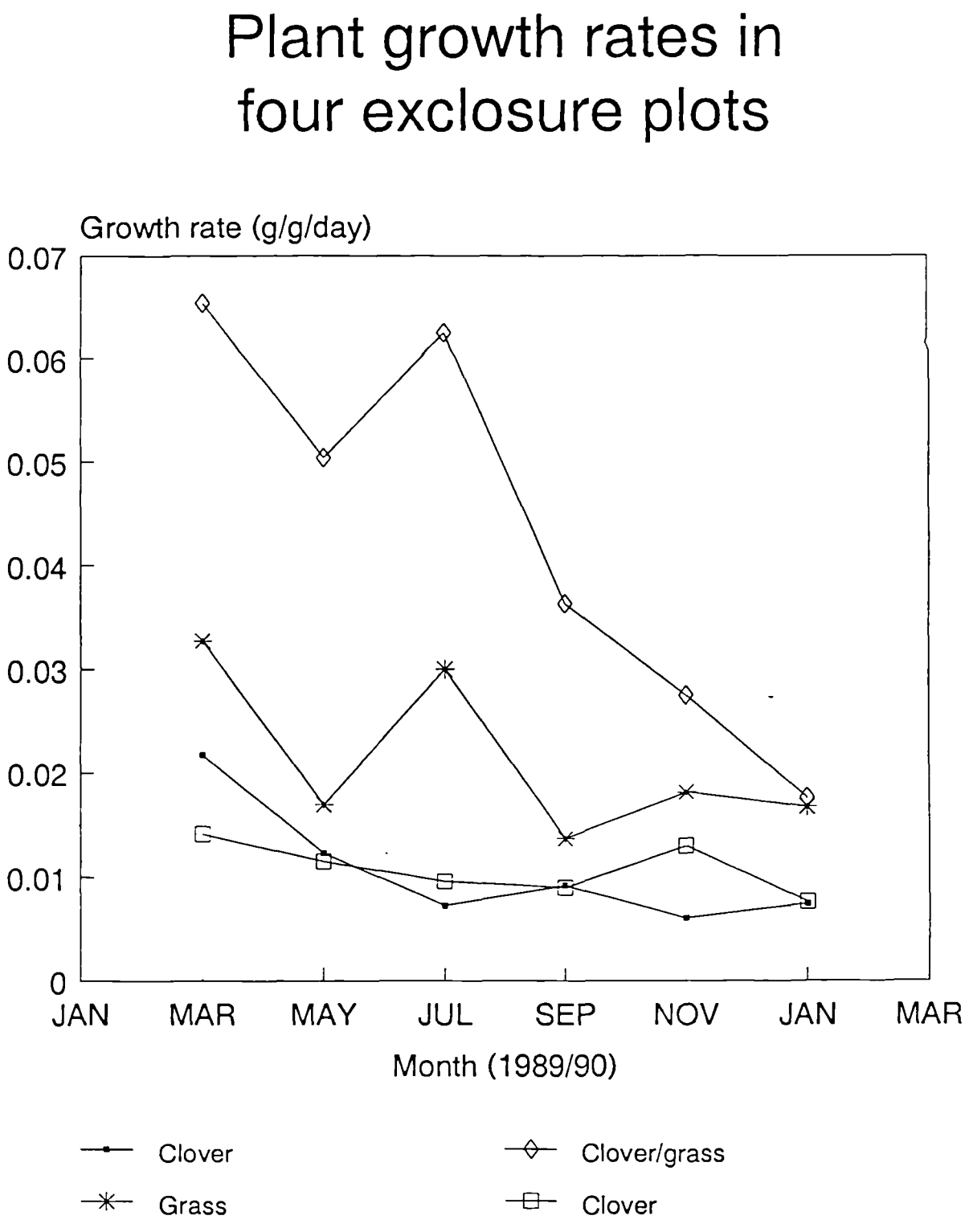


Figure 5.2 The relative growth rate of plant types in four exclosure plots clipped at two monthly intervals throughout the year. The two clover plots were located in the Saddle zone, the grass plot located in a short grass meadow and the clover/grass plot was located in a long grass meadow. The clover/grass measure is a measure of the clover type plants growing amongst the long grass.

The growth rate of *Festuca engleri* and *Carex bequaertii* also showed no real pattern with climatic variables and a mean growth rate was taken for these species of 0.017 $gg^{-1}d^{-1}$ and 0.0021 $gg^{-1}d^{-1}$ respectively.

The initial growth rates of the four plots when compared with the vegetation outside after fencing for three months were:

1. First clover plot: 0.013 $gg^{-1}d^{-1}$.
2. Second clover plot: 0.015 $gg^{-1}d^{-1}$.
3. Short grass plot: 0.023 $gg^{-1}d^{-1}$.
4. Long grass plot: 0.022 $gg^{-1}d^{-1}$.

There was therefore some increase in the relative growth rate on the initial clipping for all plots but particularly for the two grass plots but this declined as clipping continued. Growth rate in terms of mass increase per unit area also increased after the first clipping apart from the second clover plot:

	Before clipping	After clipping
1.First clover plot:	0.80 $gm^{-2}d^{-1}$.	1.36 $gm^{-2}d^{-1}$.
2.Second clover plot:	0.78 $gm^{-2}d^{-1}$.	0.74 $gm^{-2}d^{-1}$.
3.Short grass plot:	0.63 $gm^{-2}d^{-1}$.	0.92 $gm^{-2}d^{-1}$.
4.Long grass plot:	0.13 $gm^{-2}d^{-1}$.	0.39 $gm^{-2}d^{-1}$.

5.3.2 Trampling damage

The percentage of each habitat which consisted of path or flattened vegetation is given in Table 5.1. The flattening by gorillas in the Brush ridge habitat type was mainly damage to *Senecio mariettae*, which does not form a food item of any of the animals, so that its regeneration was not measured. Elephant flattened areas were still

Table 5.1 The percentage area of each habitat that was in a state of flattening by the three largest herbivores or was maintained as a path with no plant cover. Some habitats did not show signs of flattening or did not contain paths and hence are not included here. These data were calculated by measuring areas of flattened/damaged vegetation across randomly placed transects.

Path.

	Dec.-Feb.	Mar.-May	Jun.-Aug.	Sep.-Nov.
Bamboo	0.02	0.33	0.59	0.36
Saddle	0.62	0.47	0.05	1.02
Herbaceous	0.82	0.52	1.02	0.59
Brush Ridge	1.07	0.55	1.13	0.83
Giant Lobelia	0.31	0.11	0.24	0.10
Alpine	0.04	0.00	0.09	0.13
Karisimbi meadows	0.18	0.21	0.31	0.14

Gorilla flattened path.

	Dec.-Feb.	Mar.-May	Jun.-Aug.	Sep.-Nov.
Bamboo	0.00	0.47	0.02	0.57
Saddle	0.15	0.10	0.13	0.24
Herbaceous	3.22	2.39	0.70	2.63
Brush Ridge	0.03	0.47	0.14	0.58

Buffalo flattened path.

	Dec.-Feb.	Mar.-May	Jun.-Aug.	Sep.-Nov.
Bamboo	0.03	0.36	0.01	0.19
Saddle	0.39	0.27	0.05	0.31
Herbaceous	0.89	0.49	0.60	0.56

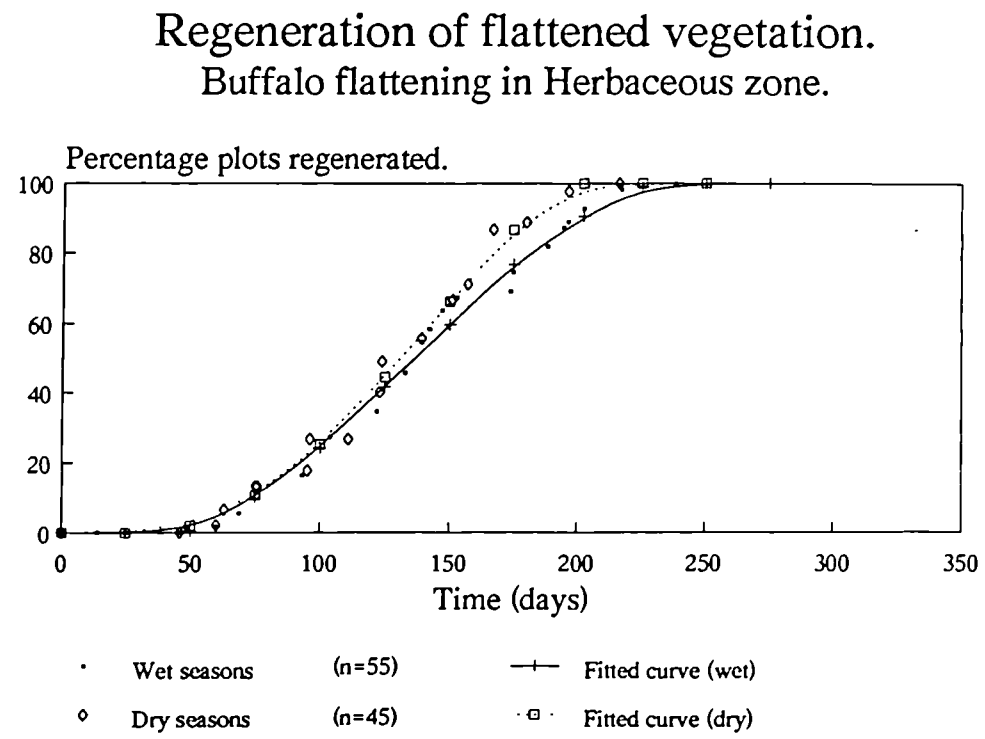
Elephant flattened path.

	Dec.-Feb.	Mar.-May	Jun.-Aug.	Sep.-Nov.
Bamboo	-	-	0.95	0.54
Saddle	-	-	0.34	0.44
Herbaceous	-	-	0.61	0.90

visible in September-November despite the fact that elephant were not in the study area at this time.

Regeneration of flattened vegetation tended to be sigmoidal, similar to a logistic growth curve (see Figures 5.3 to 5.5). However it was found that a polynomial provided a better fit (Table 5.2). Polynomials have been fitted to growth equations of plants before (Hughes & Freeman 1967). In order to test between differences in regeneration rates for different seasons it is necessary to try and linearise the fitted lines and to use the test provided by Mead & Curnow (1983) which can measure differences between straight lines. The logistic equation can be plotted in a linear form and therefore tests were calculated using these curves. These showed significant differences between wet and dry seasons growth for all habitats and animal species except for the gorilla flattening in the Saddle habitat type (Gorilla: Herbaceous: $F=5.06$, d.f.=2,41, $P<0.05$; Saddle: F==3.07, d.f.=2,39, P=ns; Buffalo: Herbaceous: $F=3.34$, d.f.=2,34, $P<0.05$; Saddle: $F=9.17$, d.f.=2,27, $P<0.005$) As the polynomials form an even closer fit to the points (because the residual sum of squares is much lower) it is probable that these differences are real. Tests were also done with the combined regeneration data for wet and dry seasons between the Saddle and Herbaceous zones; both showed significant differences (Gorilla: $F=16.0$, d.f.=2,87, $P<0.005$; Buffalo: $F=5.62$, d.f.=2,57, $P<0.01$)

Buffalo and gorilla damage however took approximately the same amount of time to regenerate for all plots, whilst elephant took at least another 50 days longer and up to 200 days for areas dug by the elephants tusks and feet as they looked for roots. Elephants tended to kill many of the plants they walked on whilst the other two species simply knocked the plants over, allowing them to regenerate from side shoots more quickly. Elephants also seemed to affect the floristic nature of the plant community by encouraging the growth of other species such as thistles in areas where trampling occurred, even when these plants were not in the surrounding vegetation.



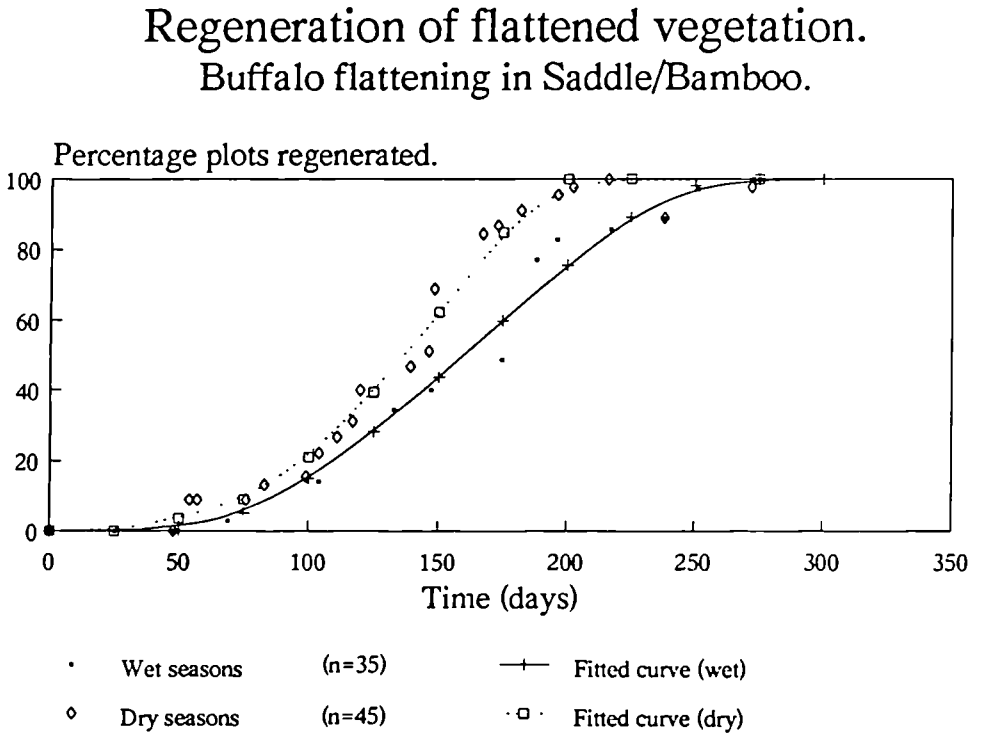
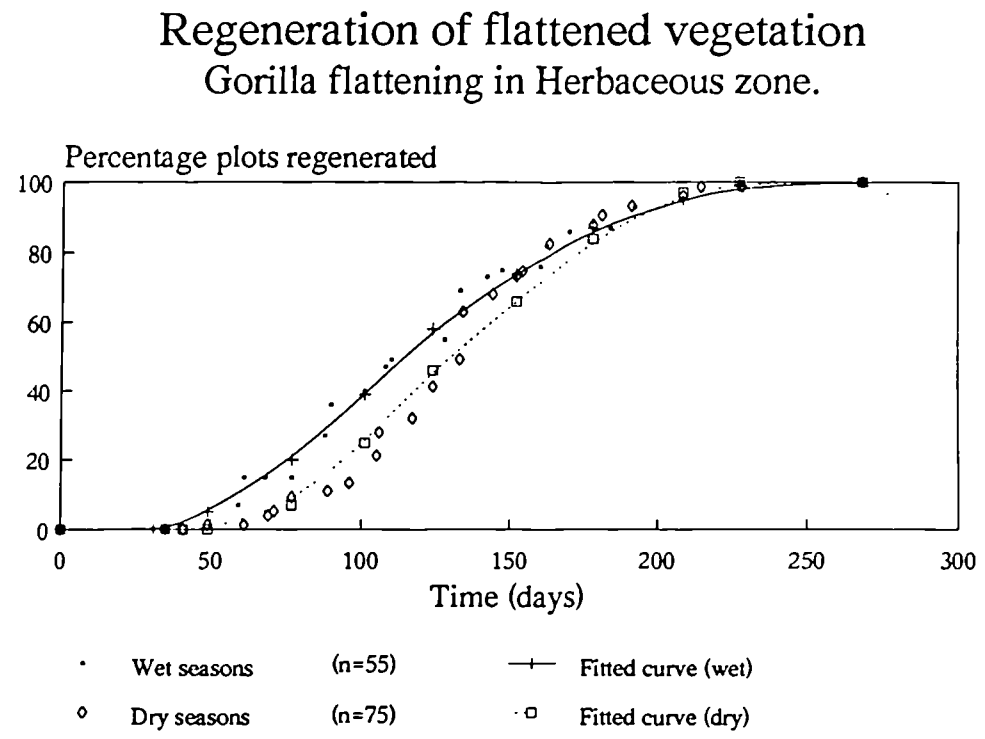


Figure 5.3 The regeneration of vegetation flattened by buffalo. The percentage of plots considered as completely regenerated are plotted against the number of days since the flattening occurred. The regeneration of plots flattened in the wet and dry seasons are plotted separately for the Saddle/Bamboo and Herbaceous zones.



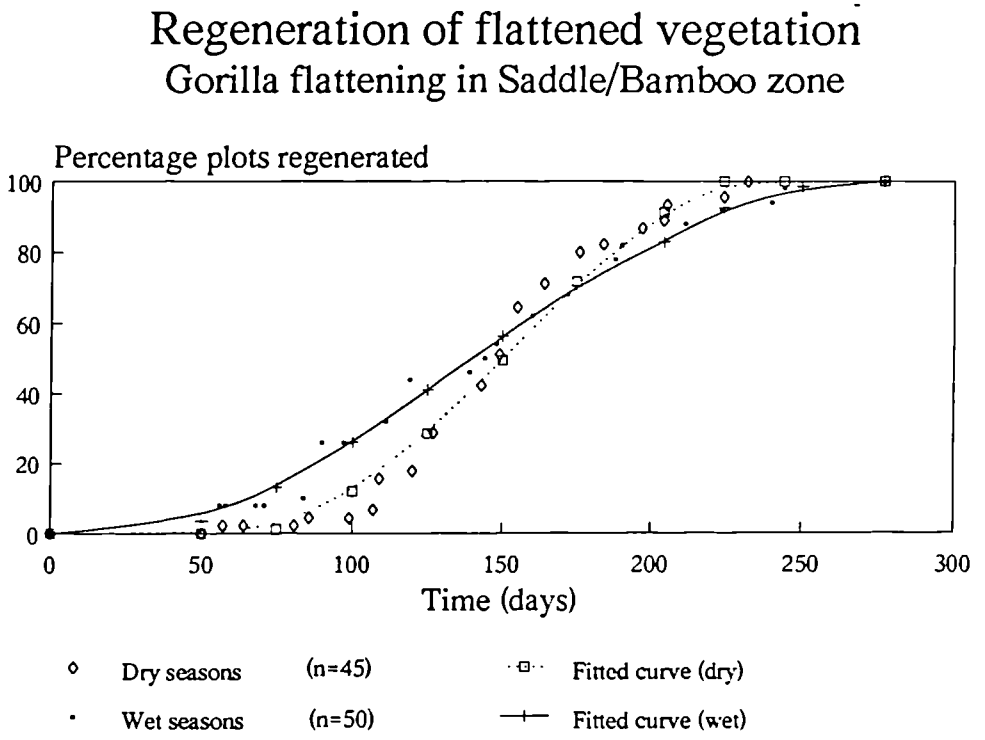
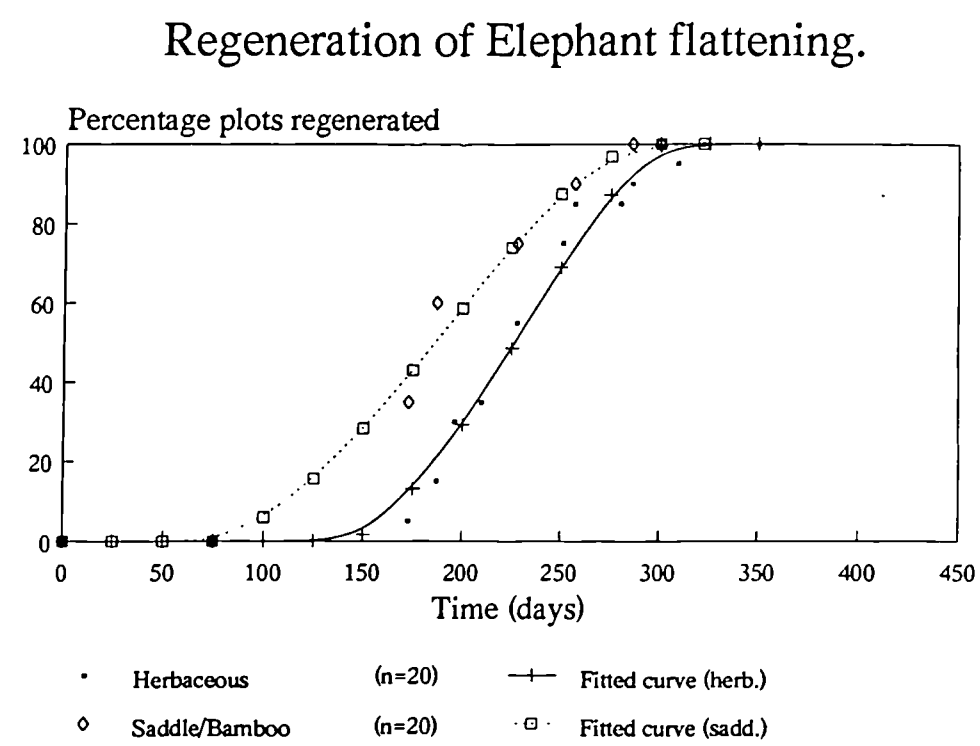


Figure 5.4 The regeneration of vegetation flattened by gorillas. The percentage of plots considered as completely regenerated are plotted against the number of days since the flattening occurred. The regeneration of plots flattened in the wet and dry seasons are plotted separately for the Saddle/Bamboo and Herbaceous zones.



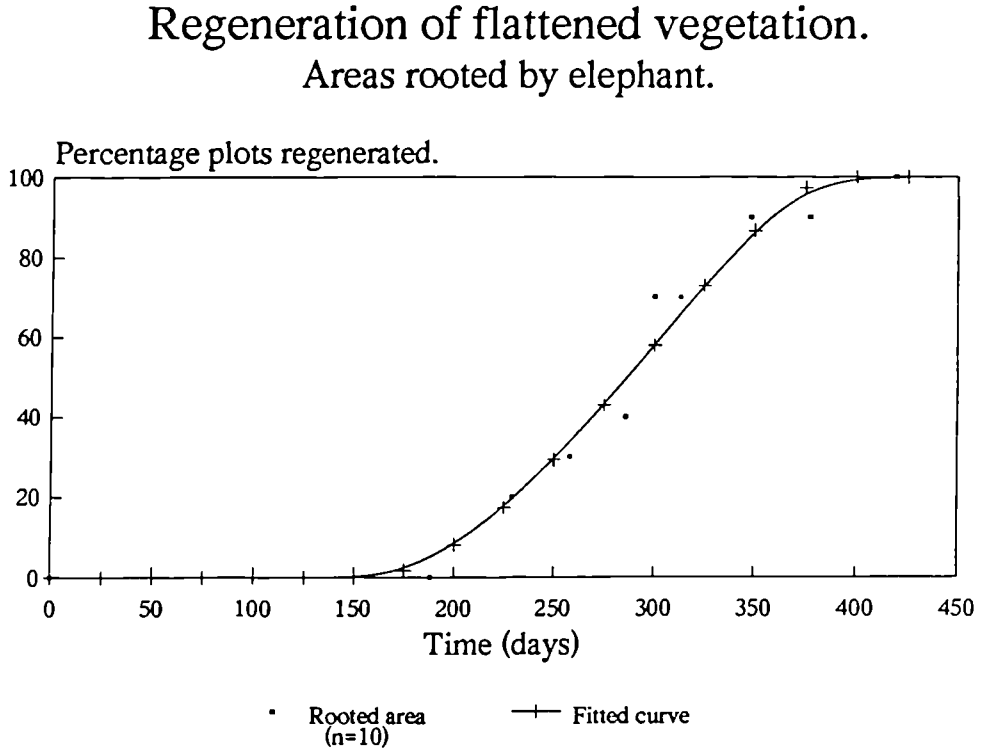


Figure 5.5 The regeneration of vegetation flattened by elephants. The percentage of plots considered as completely regenerated are plotted against the number of days since the flattening occurred. The regeneration of plots flattened in the Saddle/Bamboo and the Herbaceous zones are plotted separately for the June-August dry season 1988 when elephant were in the study area. The rate of regeneration of plots dug or rooted by the elephant are also given.

Table 5.2 The polynomial equations fitted to the regenerating vegetation trampled by the three largest herbivores. The equations are of the form: $y=ax^4+bx^3+cx^2+dx+e$ where y=percentage number of plots fully regenerated and x= time in days. Sample size (n) is also given.

	Season	a (10^{-8})	b (10^{-5})	c (10^{-2})	d	e	n
Gorilla							
Herbaceous	wet	9.3	-6.7	1.5	-0.50	1.34	55
	dry	7.3	-6.4	1.7	-0.89	4.74	75
	total	8.6	-6.9	1.6	-0.78	2.81	130
Saddle	wet	1.6	-2.2	0.7	-0.24	0.77	50
	dry	-12.2	3.7	0.09	-0.25	3.19	45
	total	0.1	-1.9	0.8	-0.48	3.81	95
Buffalo							
Herbaceous	wet	-1.1	-1.6	0.8	-0.38	2.22	55
	dry	-14.9	4.1	0.07	-0.08	0.36	45
	total	-3.0	-93.4	0.7	-0.40	2.41	100
Saddle	wet	-2.6	0.09	0.4	-0.24	1.65	35
	dry	-25.1	9.0	-0.6	0.22	-0.91	45
	total	-1.1	-1.2	0.7	-0.42	1.70	80
Elephant							
Herbaceous		-8.9	5.2	-0.7	0.23	0.02	20
Saddle		-3.1	0.9	0.2	-0.18	0.04	20
Dug area		-2.9	2.2	-0.3	0.18	-0.14	10

In order to calculate the amount of vegetation flattened per day, a model similar to the one for dung decay in Chapter 3 was used. If it is assumed that flattening is constant over one season and is regenerating in the form of the polynomial given in Table 5.2, then the proportion of vegetation flattened at the end of one season is equal to the area between the polynomial curve and the Y-axis of the graphs in Figures 5.3-5.5 (up to the number of days in the season). The Y-axis must be measured in proportions rather than percentages for this to be the case. The amount of vegetation flattened per day multiplied by this area will give the amount of flattening expected in that season. Similarly the proportion flattened by the end of the second season of this first seasons flattening is equal to the area above the curve between the number of days for the first and second seasons. Integrating the polynomial formulae gives the area under the curve which can be subtracted from the total area possible (i.e if there was no regeneration) to give the area above the curve. The integral of the basic formula is as follows:

$$\int_0^T ax^4+bx^3+cx^2+dx+e = \left[\frac{ax^5}{5} \quad +\frac{bx^4}{4} \quad +\frac{cx^3}{3} \quad +\frac{dx^2}{2} \quad +ex \right]_0^T$$

When integrating the curves the equations were taken from where the main curve left the X-axis because the formulae given in Table 5.2 cross the X-axis near the origin.

This process gives the proportion that remains flattened each season from each particular season of flattening. A similar process to the dung decay model is undertaken where the amount of flattening per day is estimated for each season and the actual amount of vegetation in a state of flattening is calculated. This is then compared with the measure obtained from the transects and the estimate of the amount flattened per day is corrected by the ratio of these two. The whole process then continues to iterate until a stable point is reached; the actual amount of vegetation flattened per day.

This area is given for each animal species and habitat type in Table 5.3 in terms of $m^2ha^{-1}d^{-1}$. Standard errors of the measured flattening were calculated using a modification of an equation given by Burnham, Laake & Anderson (1980) for the variance of strip transect data and the upper and lower limits put into the model. The modified equation is as follows (K.P. Burnham pers. comm.):

$$Var(D) = \frac{\Sigma A_i[(n_i/A_i)-D]^2}{A(R-1)}$$

A_i = Area of ith transect

n_i = Area flattened on ith transect

R = Number of strip transects

D = Mean area flattened per square metre

A = Total area of all transects

Finally the amount of vegetation flattened per day was related to the number of animals found from the faecal counts given in Chapter 3. To maximise the sample size, flattening damage was related to the estimated population size of each herbivore in all habitats. From the vegetation survey it was calculated that 18.6% of the Bamboo, 55.6% of the Saddle and 100% of the Herbaceous zone would show flattening. If the areas of each habitat are taken into account this means that 47% of the study area would show flattening. In order to relate the amount of flattening to the numbers of animals present, the habitats must be equal in their ability to show flattening. Therefore the area flattened per day for each habitat and herbivore was multiplied by the ratio of 100/(percentage area that would show flattening). Regressing these transformed areas of flattening damage against the number of animals produced significant regressions (Figure 5.6). The equations of these lines are given in Table 5.4. There was some scatter but this was not surprising as the animals move around in groups and often follow each others trails, so that flattening

Table 5.3 The area of vegetation flattened each day by the three large herbivores in the three main habitats to show flattening. Figures given are the area flattened daily per hectare ($m^2 day^{-1} ha^{-1}$) and were determined using the data on the percentage area flattened (Table 5.1) and the regeneration rate of flattened vegetation using a model described in the text. Standard errors are given in parentheses.

Buffalo.

	Dec.-Feb.	Mar.-May	Jun.-Aug.	Sep.-Nov.
Bamboo	**0.00**	**0.38** (±0.05)	**0.00**	**0.16** (±0.05)
Saddle	**0.23** (±0.02)	**0.14** (±0.01)	**0.00**	**0.33** (±0.02)
Herbaceous	**0.83** (±0.10)	**0.14** (±0.04)	**0.60** (±0.08)	**0.36** (±0.04)

Gorilla.

	Dec.-Feb.	Mar.-May	Jun.-Aug.	Sep.-Nov.
Bamboo	**0.00**	**0.48** (±0.13)	**0.00**	**0.62** (±0.10)
Saddle	**0.06** (±0.005)	**0.06** (±0.02)	**0.11** (±0.02)	**0.20** (±0.03)
Herbaceous	**2.54** (±0.17)	**1.49** (±0.05)	**0.17** (±0.07)	**3.03** (±0.14)

Elephant.
(Residence time of 108 days)

	Jun.-Aug.	Sep.-Nov.
Bamboo	**0.88** (±0.14)	**0.50** (±0.08)
Saddle	**0.32** (±0.04)	**0.40** (±0.04)
Herbaceous	**0.56** (±0.12)	**0.84** (±0.11)

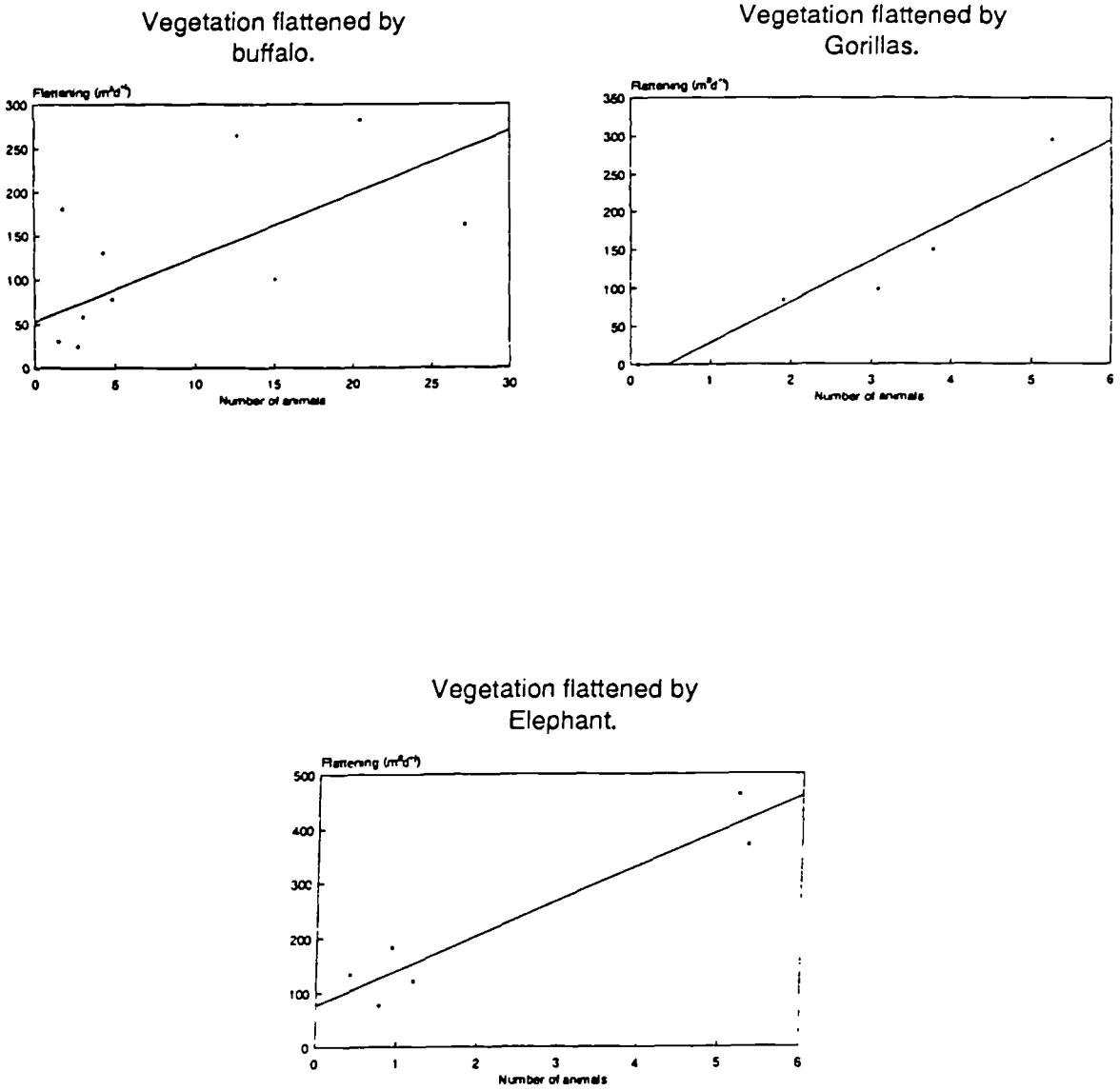


Figure 5.6 The regression of the rate of flattening by each of the three largest herbivores against the number of animals. Flattening rate (m^2d^{-1}) is determined in Table 5.3 and the number of animals during each season are given in Chapter 3.

Table 5.4 The linear regression equations relating the area of vegetation flattened per day to the number of animals present. The formula is of the form $y=ax+b$ (where y=area flattened per day and x=number of animals) and the number of samples, the adjusted regression coefficient and the probability of the fit are given.

Species	a	b	n	R^2_{adj}	P<
Buffalo	7.24	52.74	12	39.3	0.05
Gorilla	53.29	-24.55	5	87.7	0.05
Elephant	63.80	77.10	6	87.8	0.01

Table 5.5 The area (m^2) of vegetation flattened each day in the study area by the three largest herbivores. The table shows the total flattening damage in the three habitat types (using the measures that 18.6% of the Bamboo, 55.6% of the Saddle and 100% of the Herbaceous zones would show flattening damage).

Species	Animal number	Bamboo	Saddle	Herbaceous	Total
Buffalo	34	12	104	76	192
Gorilla	13	10	5	289	304
Elephant	1	15	70	88	173
Total		37	179	453	669

is reduced. Within the study area the total area of vegetation flattened per day was calculated for each species and habitat type using these equations and taking into account the percentage area of the habitat that would show flattening (Table 5.5).

5.4 Discussion

5.4.1 Productivity

Most studies on plant productivity measure it in terms of biomass increase per unit area per unit time ($gm^{-2}d^{-1}$) (McNaughton 1979, Pellew 1983). This method is only really suitable where the plant diversity is low and the habitat uniform. A more suitable measure is that used here, although there are few studies which have used this measure and with which comparisons can be made. Prins (1987) used this measure for grasses in Lake Manyara National park and obtained values of 0.1-0.5 $gg^{-1}d^{-1}$, which he stated were close to the optimal growth rates for African grasses. These figures are about three times the maximum value for grasses at Karisoke, which is not unreasonable given the lower temperatures experienced at this altitude. McNaughton (1985) found values of 0.04-0.08 $gg^{-1}d^{-1}$ in the Serengeti depending upon the extent of grazing that occurred in the area. The values of 0.022 $gg^{-1}d^{-1}$ for grass that had not been clipped is probably more realistic for the bulk of the grass in the Birungas rather than the maximum value of 0.04 $gg^{-1}d^{-1}$. The growth rate of *Festuca engleri*, which was measured at 3300m, is lower than this at a mean value of 0.017 $gg^{-1}d^{-1}$. This may also be due to a temperature drop associated with a 200m rise in altitude (Spinage 1972).

As has been found for other studies the growth responses of plants in the Birungas were variable. The results of the productivity measures for the tall herbs showed that as a plant became taller its rate of biomass increase slowed down. This may be one

result of plant competition, since it would pay these tall herbs to grow quickly up into the light and then to invest more in root production and reproduction. Ruess & McNaughton (1984) showed that after clipping grass, investment by the plant was increased in leaf tissue over root tissue. Rice & Bazzaz (1989) showed that the plant height-mass relationship for the herb *Abutilon theophrasti* varied depending on the light conditions experienced by the plant. At low or high light levels the relationship was linear when both logged values of height and mass are plotted. However plants grown in low light and transferred to high light showed a curvilinear response which would be similar to the height-mass equations found here (Appendix 2). Therefore it is possible that relatively low light levels are competitively inhibiting plant growth and hence there is a need to invest more in the initial stages of growth. Competition may also explain the high degree of scatter in the growth rates of the smaller plants in Figure 5.1.

The results of the clipped exclosure plots showed a general decline in growth rate with each subsequent clipping. This did not correlate with any climatic variables measured, and was more likely to be due to an effect of trampling during the clipping process and the simulation of heavy grazing. The clipping process may also select for prostrate growth morphs of certain plant species which would mean that less plant material was clipped each time. The growth rate of each plot increased after the first clipping (although the clover plots did not increase significantly) over the initial growth rate that was measured when the plot was first fenced. This was a similar response to that found by Ruess & McNaughton (1984). The highest growth rates came from the herbs in the long grass, but they also showed the fastest decline with heavy clipping, suggesting that they needed to invest heavily in new growth to reach the light and hence could not sustain constant clipping.

The productivity results obtained here appear to be realistic when compared with other ecosystems and therefore were used in the model in Chapter 6.

5.4.2. Trampling damage

Watts (1983) calculated that regeneration of tall herbs after flattening by gorillas would take between 200 and 260 days. He assumed an exponential rise in the regeneration of the plants rather than the sigmoidal increase as was found here. This would explain why the measured value of 260-280 days was slightly higher. Buffalo flattened areas regenerated at a similar rate to the gorillas. However, since the buffalo seem to use a lot of the same trails (pers. obs.), the actual amount flattened is relatively small given the high numbers of animals in the study area (Table 5.5). Where trails were used regularly no vegetation grew as the soil was churned up too much by the hooves of these animals. Each elephant flattened a lot of vegetation (Table 5.5) and this may explain why these animals did not stay long in an area.

The regression equations in Table 5.4 and Figure 5.6 relating flattening damage to animal numbers were based on relatively few points for both gorillas and elephants, because they were not present for all seasons in all habitat types. Hence single points could have a significant effect on the final result. Watts (1983) calculated that the mean distance travelled by the gorilla group he studied was 506m d^{-1}. In the herbaceous zone this dropped to 485m d^{-1}. A value of 304m^2 flattened d^{-1} by gorillas (Table 5.5) therefore would seem to be reasonable, since they spent about 30% of their time in the study area and also visited areas where the vegetation would not show flattening. Three estimates were obtained by following all the gorilla trails between consecutive night nests and measuring the area flattened. This was done for Beetsme's group where the number of animals (12) was similar to the mean density in the study area. These gave a value of 552m^2 flattened d^{-1} in the Herbaceous zone. The percentage of the study area which would show flattening is 47% which would mean that if the habitats were used evenly, 259m^2 of vegetation would be flattened d^{-}

^{1} and with the mean percentage use by the gorillas of each habitat (Chapter 3) this works out at 299m^2 d^{-1}, a very close agreement to the 304m^2 d^{-1} obtained above.

In conclusion the productivity of plants in the Birungas would appear to be lower when compared with other sites in Africa, and this is probably due to the more temperate climate experienced here. At the same time the large herbivores were trampling 669m^2 of tall herbaceous vegetation per day. However this formed only 0.0055% of the total study area and 0.0115% of the tall herbaceous vegetation. Since the recovery rate of the vegetation required 260-400 days depending on the animal causing the damage, it would appear that the impact of these herbivores on the environment could easily be sustained. This conclusion does however assume that all plant species were evenly spread in the tall herbaceous areas rather than patchily distributed, as was shown in Chapter 2. Hence if the herbivores were selectively using certain patches of vegetation, the flattening damage they caused could possibly have a greater impact.

CHAPTER SIX

HERBIVORE-PLANT INTERACTIONS IN THE BIRUNGAS

6.1 Introduction

The main aim of this thesis was to determine what impact each of the herbivore species had upon the vegetation in the Birungas. Once this had been calculated, the data could be used to assess whether these species were adversely affecting the mountain gorilla population through "exploitative competition" (Schoener 1983). Competition between species is not easy to demonstrate (Schoener 1983, Underwood 1986) and requires experimental manipulation of species numbers (Strum & Western 1982, MacNally 1983, Schoener 1983) and the use of replicate experiments (Underwood 1986). This is obviously impossible in the Birungas where all the animals are protected and it is the only high altitude montane park to contain mountain gorillas. Therefore any inference of the impact of one of these herbivores upon another must assume that some form of competition was occurring.

The lack of predators in the Birungas meant that the herbivore populations could not be limited by secondary consumers and so it was likely to be the food supply which limited or will limit the populations. Therefore it is possible that now or in the future, competition could occur between herbivores for a limited food resource.

Gause's "competitive exclusion principle" has nowadays been replaced by a "competitive niche shift principle" (Den Boer 1986) which states that where competition occurs one or both species will shift their niches to avoid too great an overlap. A starting point therefore in the investigation of competition between these

herbivores would be to measure the degree of overlap found in their respective habitats.

6.2 Niche overlap

6.2.1 Measurement

There is much controversy about the use of niche overlap measures because in the past they have been used as a measure of competition between species (Lawlor 1980). A high overlap can be used to infer that competition is present because both niches overlap greatly, or it can be used to infer that competition is not present because the niches would be expected to shift if this were the case (Giller 1984). A low overlap may mean that competition is being avoided or that it was present at one time, although it may simply mean that the two species are so different that competition will not occur (Lawlor 1980).

The many niche overlap measures that exist (Hurlbert 1978, Krebs 1989) and the relative merits of each one adds to this confusion. For this study two niche overlap measures were calculated:

a. Pianka's measure (Pianka 1973): This was chosen because it is a commonly used measure and allows a comparison with other studies.

$$O_{jk} = \frac{\Sigma(P_{ij}P_{ik}}{[\Sigma(P_{ij})^2\Sigma(P_{ik})^2]^{1/2}}$$

Where: P_{ij} = Proportion of resource *i* used by species *j*.

This measure ranges from 1.0 for total overlap to zero for no overlap.

b. Hurlbert's measure (Hurlbert 1978): this measure takes the abundance of the resources being used into account:

$$O_{jk} = \sum(P_{ij}P_{ik}/a_i)$$

Where: P_{ij} = Proportion of resource *i* used by species *j*.

a_i = proportional amount of resource state *i*.

This measure is zero when the two species share no resources; 1.0 when both species utilise each resource state in proportion to its abundance; and >1.0 when the two species use certain resource states more intensively than others and the preferences of the two species tend to coincide.

6.2.2 Results

The overlap in habitat use between each of the five herbivores is shown in Table 6.1 for Pianka's measure and Table 6.2 for Hurlbert's measure. The overlap is given for each season during the year and for the mean habitat use throughout the year. Pianka's measure showed an increase in overlap between all species pairs during the wet seasons, apart from the bushbuck/duiker pairing which increased during the dry seasons. There was no obvious change in the food supply or nutrient content between seasons or a change in productivity (see Chapters 2, 4 and 5) and therefore this increased overlap may have been due to shelter from the rain and cold temperatures. This consistent variation does not appear in Hurlbert's measure however, when the availability of the habitat types is taken into account.

Table 6.3 shows the overlap (Pianka's) in the use of the vegetation types within a habitat (see Chapter 3). This assumes that where dung is deposited within a habitat

Table 6.1 Niche overlap values for the degree of habitat overlap between the herbivore species using Pianka's niche overlap index. Overlap was calculated using the proportion of the total population size in each habitat (see Chapter 3).

Gorilla niche overlap:

	Dec-Feb	Mar-May	Jun-Aug	Sep-Nov	Total
Duiker	0.630	0.763	0.630	0.763	0.714
Bushbuck	0.620	0.857	0.603	0.788	0.742
Buffalo	0.484	0.655	0.565	0.778	0.631
Elephant			0.611		0.709

Duiker niche overlap:

	Dec-Feb	Mar-May	Jun-Aug	Sep-Nov	Total
Bushbuck	0.984	0.964	0.986	0.981	0.983
Buffalo	0.905	0.949	0.901	0.963	0.946
Gorilla	0.630	0.763	0.630	0.763	0.714
Elephant			0.963		0.963

Bushbuck niche overlap:

	Dec-Feb	Mar-May	Jun-Aug	Sep-Nov	Total
Duiker	0.984	0.964	0.986	0.981	0.983
Buffalo	0.889	0.900	0.878	0.981	0.939
Gorilla	0.620	0.857	0.603	0.788	0.742
Elephant			0.993		0.994

Buffalo niche overlap:

	Dec-Feb	Mar-May	Jun-Aug	Sep-Nov	Total
Duiker	0.905	0.949	0.901	0.963	0.946
Bushbuck	0.889	0.900	0.878	0.981	0.939
Gorilla	0.484	0.655	0.565	0.778	0.631
Elephant			0.865		0.927

Table 6.2 Niche overlap values for the degree of habitat overlap between the herbivore species using Hurlbert's niche overlap index. Overlap was calculated using the proportion of the total population size in each habitat (see Chapter 3) and takes into account the availability of each habitat type.

Gorilla niche overlap:

	Dec-Feb	Mar-May	Jun-Aug	Sep-Nov	Total
Duiker	0.876	0.823	0.876	0.823	0.852
Bushbuck	0.800	0.975	0.779	0.884	0.888
Buffalo	0.391	0.845	0.541	1.088	0.598
Elephant			0.737		0.912

Duiker niche overlap:

	Dec-Feb	Mar-May	Jun-Aug	Sep-Nov	Total
Bushbuck	1.043	0.985	1.058	1.026	1.027
Buffalo	1.136	1.123	1.110	0.993	1.091
Gorilla	0.876	0.823	0.876	0.823	0.852
Elephant			0.982		0.982

Bushbuck niche overlap:

	Dec-Feb	Mar-May	Jun-Aug	Sep-Nov	Total
Duiker	1.043	0.985	1.058	1.026	1.027
Buffalo	0.979	0.944	0.929	1.060	0.998
Gorilla	0.800	0.975	0.779	0.884	0.888
Elephant			1.224		1.177

Buffalo niche overlap:

	Dec-Feb	Mar-May	Jun-Aug	Sep-Nov	Total
Duiker	1.136	1.123	1.110	0.993	1.091
Bushbuck	0.979	0.944	0.929	1.060	0.998
Gorilla	0.391	0.845	0.541	1.088	0.598
Elephant			0.862		1.020

Table 6.3 The degree of niche overlap (Pianka's measure) between herbivore species in the use of vegetation types within each habitat. This was based on data of faecal deposition in each vegetation type (eg. nettles, clover).

Duiker niche overlap:

	Bushbuck	Buffalo	Gorilla	Elephant
Bamboo	0.950	0.795	0.888	0.926
Saddle	0.977	0.606	0.750	0.918
Meadow	0.783	0.743		0.703
Herbaceous	0.937	0.866	0.869	0.640
Brush ridge	0.960		0.464	
Giant Lobelia	0.988		0.934	
Alpine	0.986	0.745		
Karisimbi meadows	0.967	0.926		

Bushbuck niche overlap:

	Duiker	Buffalo	Gorilla	Elephant
Bamboo	0.950	0.849	0.920	0.927
Saddle	0.977	0.650	0.706	0.924
Meadow	0.783	0.997		0.985
Herbaceous	0.937	0.946	0.930	0.803
Brush ridge	0.960		0.402	
Giant Lobelia	0.988		0.953	
Alpine	0.986	0.728		
Karisimbi meadows	0.967	0.979		

Buffalo niche overlap:

	Duiker	Bushbuck	Gorilla	Elephant
Bamboo	0.795	0.849	0.964	0.719
Saddle	0.606	0.650	0.238	0.430
Meadow	0.743	0.997		0.992
Herbaceous	0.866	0.946	0.884	0.815
Alpine	0.745	0.728		
Karisimbi meadows	0.926	0.979		

Gorilla niche overlap:

	Duiker	Bushbuck	Buffalo	Elephant
Bamboo	0.888	0.920	0.964	0.808
Saddle	0.750	0.706	0.238	0.821
Herbaceous	0.869	0.930	0.884	0.652
Brush ridge	0.464	0.402		
Giant Lobelia	0.934	0.953		

reflects the microhabitat utilisation of that species. The values obtained in Table 6.3 were weighted by the area of each habitat type to produce a single overlap measure for each species pair. The product of this and the yearly habitat overlap gives a measure of the total habitat overlap on a more detailed scale (Table 6.4). These values all show a reduction in overlap if microhabitat is taken into account.

The two measures of dietary overlap are shown in Table 6.5. The figures for Pianka's dietary overlap are much lower than the habitat overlap. Hurlbert's measure showed that nearly all species pairs were using similar food items in greater proportion to the proportional abundance of food in the study area. This means that there were some plant species which were little touched by most of the species. Finally Table 6.6 shows the combined overlap (Pianka's) of diet and habitat, and diet, habitat and microhabitat. These show quite low values when compared with other studies (Walker 1979).

If these overlap measures are to be interpreted in any meaningful way it is necessary to have a measure of what might be expected if the habitats or food plants were used at random. Joern & Lawlor (1980) describe a technique where Monte Carlo analyses of randomly constructed communities are used to obtain predicted values of niche overlap with which the actual values can be compared. This was done for both the habitat overlap and for the dietary overlap using the data from this study. It was assumed that all species could use all habitats, and random numbers were generated for the proportional use of each habitat by two species. The overlap (Pianka's) between the species was then calculated and the process repeated 200 times. The mean overlap value obtained was 0.761 (Variance = 0.116). The same process was performed 100 times for the use of the 36 dietary items to give a mean overlap of 0.758 (Variance = 0.056). This was not very meaningful, however, because elephants could not physically eat clover-like plants and therefore not all plant species were available to each herbivore. Hence this process was repeated for species pairs keeping

Table 6.4 A comparison of the degree of overlap (Pianka's index) between species for habitat use and for vegetation use within a habitat. The former measure was based on the mean overlap throughout the year (Table 6.1). The latter measure weighted overlap values given in Table 6.3 by the proportional area of each habitat to give an overall overlap value. The product of these values gives a measure of habitat overlap when examined on a finer scale.

Habitat overlap: (H)

	Duiker	Bushbuck	Buffalo	Gorilla	Elephant
Duiker	1.000				
Bushbuck	0.984	1.000			
Buffalo	0.946	0.939	1.000		
Gorilla	0.714	0.742	0.631	1.000	
Elephant	0.963	0.994	0.927	0.709	1.000

Weighted overlap of vegetation use within a habitat: (V)

	Duiker	Bushbuck	Buffalo	Gorilla	Elephant
Duiker	1.000				
Bushbuck	0.964	1.000			
Buffalo	0.699	0.753	1.000		
Gorilla	0.763	0.745	0.420	1.000	
Elephant	0.845	0.897	0.548	0.779	1.000

Combined habitat overlap: (H x V)

	Duiker	Bushbuck	Buffalo	Gorilla	Elephant
Duiker	1.000				
Bushbuck	0.948	1.000			
Buffalo	0.661	0.707	1.000		
Gorilla	0.545	0.553	0.265	1.000	
Elephant	0.814	0.892	0.508	0.552	1.000

Table 6.5 The degree of overlap in the dietary intake of each herbivore species giving the values for Pianka's and Hurlbert's indices of overlap. The overlap values were calculated from the proportional intake of the 36 plant species or plant species groupings given in Chapter 4.

Pianka's measure:

	Duiker	Bushbuck	Buffalo	Gorilla	Elephant
Duiker	1.000				
Bushbuck	0.657	1.000			
Buffalo	0.282	0.419	1.000		
Gorilla	0.174	0.195	0.086	1.000	
Elephant	0.051	0.140	0.198	0.508	1.000

Hurlbert's measure:

	Duiker	Bushbuck	Buffalo	Gorilla
Bushbuck	6.791			
Buffalo	3.026	3.721		
Gorilla	1.126	1.445	1.862	
Elephant	0.177	2.107	4.987	7.308

Table 6.6 The degree of niche overlap between the herbivore species using the product of habitat and dietary overlap (Pianka's measure). This overlap was calculated with and without the overlap in the use of vegetation types within a habitat (Table 6.4).

Diet overlap x Habitat overlap:

	Duiker	Bushbuck	Buffalo	Gorilla	Elephant
Duiker	1.000				
Bushbuck	0.646	1.000			
Buffalo	0.267	0.393	1.000		
Gorilla	0.124	0.145	0.054	1.000	
Elephant	0.049	0.139	0.184	0.360	1.000

Diet overlap x Habitat overlap x Vegetation overlap within a habitat type:

	Duiker	Bushbuck	Buffalo	Gorilla	Elephant
Duiker	1.000				
Bushbuck	0.623	1.000			
Buffalo	0.186	0.296	1.000		
Gorilla	0.095	0.108	0.023	1.000	
Elephant	0.042	0.125	0.101	0.280	1.000

Table 6.7. Expected dietary niche overlap values (Pianka's measure) predicted from Monte Carlo analysis, with those plant species currently avoided as zeros. Variances of each value are given for 100 estimates.

Expected value:

	Duiker	Bushbuck	Buffalo	Gorilla	Elephant
Duiker	1.000				
Bushbuck	0.653	1.000			
Buffalo	0.498	0.581	1.000		
Gorilla	0.427	0.456	0.376	1.000	
Elephant	0.391	0.452	0.306	0.515	1.000

Variance:

	Duiker	Bushbuck	Buffalo	Gorilla	Elephant
Bushbuck	0.075				
Buffalo	0.073	0.078			
Gorilla	0.082	0.082	0.089		
Elephant	0.076	0.084	0.074	0.094	

Table 6.8. The significant differences between the expected niche overlap values (Pianka's measure) obtained from Monte Carlo analysis and those actually measured. The number of random runs generated are given in parentheses. (Asterisks show that the degree of overlap is greater than expected, hashes show that the degree of overlap is less than expected. */# = $P<0.05$, **/## = $P<0.01$, ns = not significant).

Habitat overlap: (n=200)

	Duiker	Bushbuck	Buffalo	Gorilla	Elephant
Bushbuck	**				
Buffalo	**	*			
Gorilla	ns	ns	ns		
Elephant	**	**	*	ns	

Diet overlap with all species as food items: (n=100)

	Duiker	Bushbuck	Buffalo	Gorilla	Elephant
Bushbuck	ns				
Buffalo	##	##			
Gorilla	##	##	##		
Elephant	##	##	##	##	

Diet overlap keeping those plants uneaten as zeros: (n=100)

	Duiker	Bushbuck	Buffalo	Gorilla	Elephant
Bushbuck	ns				
Buffalo	##	#			
Gorilla	##	##	##		
Elephant	##	##	#	ns	

any plant species not eaten by each herbivore as zero. The expected values for each species pair with the variances are given in Table 6.7.

The actual niche overlap values obtained can be compared with these values and are significantly different if they occur in or outside the five highest or lowest values generated by the 100 random runs (i.e. if they occur in the 95% confidence limits). Table 6.8 shows those measured overlaps which were significantly different from that expected from the Monte Carlo analyses. Apart from the gorillas there was a significantly higher overlap between species in habitat use than was expected. This would imply that the herbivores were constrained to use the lower altitude habitats (where most animals were found - Chapter 3) possibly because of a lower plant productivity at higher altitude or because of a harsher climate. The dietary overlaps were mostly significantly lower than expected even if those plant species which were not eaten were kept at zero. This could imply that at least in the past competition existed and this separated the dietary niches of these animals. Cattle were farmed in the park for a long time (Spinage 1972) until the mid 1970s, so that the pressure on the vegetation and the potential for competition could have been high even before any subsequent increase in the numbers of wild herbivores. Since most plant species were nutrient rich and had few alkaloids (Chapter 4) such factors could not have increased the separation in the herbivore diets. However, none of this proves the existence of competition and other theories could be put forward to explain the low dietary overlap.

Therefore it cannot be argued that competition does or has occurred but it can be concluded that the potential for competition between the herbivores is very much reduced through their low dietary overlap despite their unusually high overlap in their use of the available habitats.

6.3 Modelling the ecosystem

In order to assess the impact of the herbivores upon each other it was necessary to build a model of the ecosystem. This incorporated the data on food availability (Chapter 2), herbivore numbers (Chapter 3), herbivore diet (Chapter 4), plant productivity and trampling damage (chapter 5) - see Figure 6.1. With these data it was not possible to determine whether the animals were at ecological carrying capacity (Caughley 1983) because it was necessary to know what offtake of plant material was due to other herbivores such as rodents and insects and also what the rate of plant senescence was. For the purposes of this study it was assumed that the animals were at carrying capacity such that the biomass of plant material remained constant. This required a factor to be removed from the daily plant growth to account for these other processes and thereby keep the vegetation stable. By selectively increasing the population size of one herbivore it was then possible to investigate the effects this species could have on the food supply of the other species.

The model was built on the Lotus 1-2-3 spreadsheet package and contained the following assumptions:

1. All the leaf and stem biomass measures used in the model were available to all the herbivores as food. Therefore it was assumed that there were no anti-herbivore chemicals present.
2. The vegetation was stable and did not increase or decrease in biomass.
3. Any increase in the number of a herbivore species was spread over the eight habitats in the same proportion as they had been recorded.
4. Flattening by herbivores in each habitat was spread uniformly throughout the plant species which would show flattening within the habitat. Thus all tall herbs were flattened and 70% of the *Galium*, since *Galium* was found frequently in herbaceous areas.

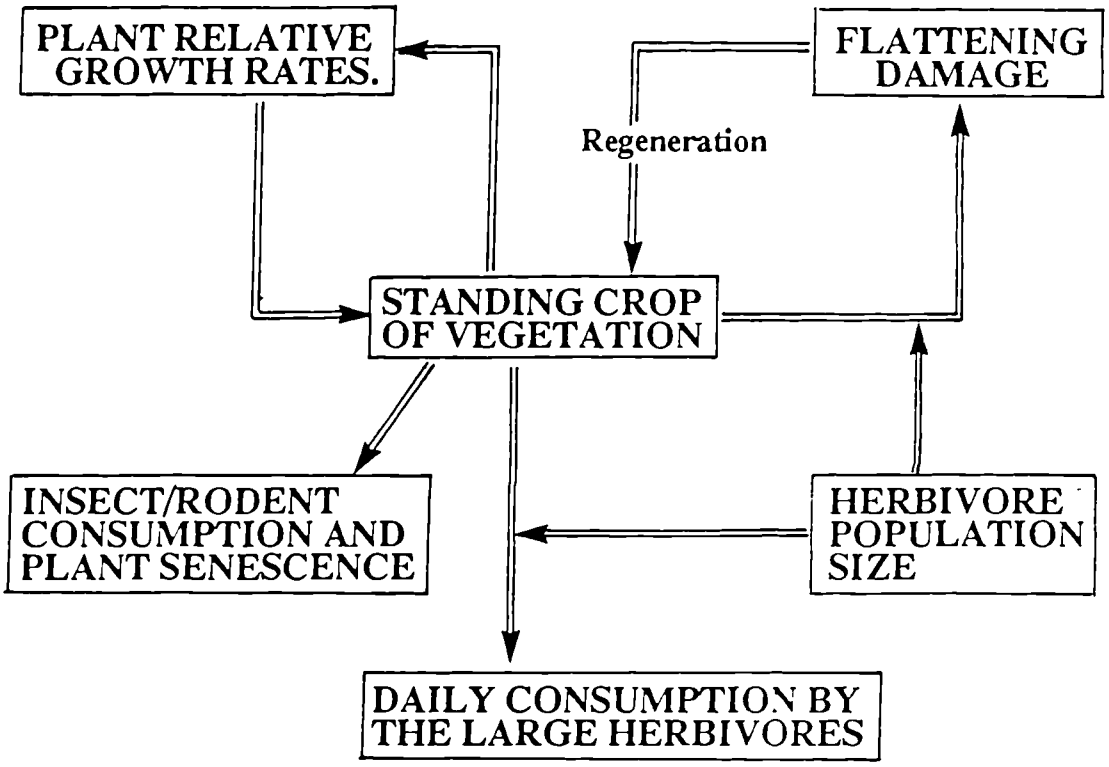


Figure 6.1. A flow chart representation of the plant-herbivore dynamics model used to analyse the effects of one herbivore upon another. All measures used are in terms of dry biomass (kg).

5. For the tall herbs it was assumed that stem density remained constant and as the mean biomass of a plant was reduced the growth rate increased following the curves given in Chapter 5. This will slightly underestimate the growth rate because the growth rate was not linear, as was assumed when obtaining the mean biomass of a plant.

6. The short herbs and grasses were given the growth rates from the first cut of the exclosure plots (i.e. the lower rate obtained after fencing an area, not the higher one obtained after clipping for the first time).

7. A reduction in plant productivity of 15% was given to the Brush Ridge and Karisimbi meadows and of 30% to the Giant *Lobelia* and Alpine zones to take into account the drop in productivity as temperature drops. The former value was obtained by comparing the productivity of *Festuca engleri* at 3300m and *Agrostis* species at 3100m, where there was a decline of 15%. The 30% drop in productivity for the top of Bisoke was obtained by assuming a linear productivity-altitude relationship.

8. If the plant biomass of a particular short herb or grass species dropped below 1000kg for the study area then plant productivity doubled to account for the increased productivity shown after clipping/grazing occurred. The tall herbs had this compensatory growth built into their growth equations.

9. If the biomass of a plant species fell below 300kg none of it was eaten or flattened by the large herbivores. This built in a simple reduction in intake as a plant species become rare, since it becomes harder to feed upon or difficult to find. The factor applied for rodent/insect damage and plant senescence was still removed however because it was still felt that these processes would continue. The mass of 300kg was chosen as this was approximately the lowest availability measure for any plant species on the study area.

10. Animal consumption was taken as 0.025xbody mass after Wijngaarden (1985) and Prins (1987) and used the masses of each species given in Chapter 3. The number of animals currently present was taken as the mean of the seasonal censuses.

Using these assumptions the model predicts the following results if the herbivores were at the numbers measured in this study:

a. Plant productivity over the whole study area was 1.06$gm^{-2}d^{-1}$ (dry mass) for an average dry mass of 148.8gm^{-2}.

b. Each herbivore population consumed the following dry mass of vegetation each day in the study area:

Duiker:	75.7kg	Bushbuck:	525.6kg
Buffalo:	273.7kg	Gorilla:	25.9kg
Elephant:	40.9kg		

This totals at 941.8kgd^{-1} or nearly one metric tonne of dry matter consumed.

c. This estimated that 8% of the primary productivity in the study area was being consumed by these five herbivores.

d. The three largest herbivores flattened 108.9kg dry mass of vegetation each day which is 0.008% of the available vegetation biomass that can be flattened.

These figures are reasonable when compared with other ecosystems. McNaughton (1985) showed that the productivity in the Serengeti averaged 3.8$gm^{-2}d^{-1}$ but it could range as high as 40$gm^{-2}d^{-1}$. Therefore 1.06$gm^{-2}d^{-1}$ would appear to be realistic in the colder climate of the Birungas. Other studies have also shown that only about 10% of the primary production is consumed by herbivores (Slobodkin, Smith & Hairston 1967, Sinclair 1975), which is in agreement with the 8% found here. Rodents and insects will add to this consumption, however, no measure of the productivity of trees and woody plants was included in this model.

Given that this model was producing credible results it was possible to look at the effects of increasing the herbivore numbers. It was decided that the model should be kept as simple as possible and that only the assumptions given above should be used. Starfield & Bleloch (1986) emphasise the importance of keeping models as simple as

possible so that the results can be interpreted intelligently. Therefore no attempt was made to build switching into the model by herbivores as food plant availability dropped because there were no data upon which to base any such decisions. If a plant species dropped below 300kg then less food in total would be consumed or flattened by the herbivores which would infer a fluctuation in the herbivore numbers. This was easier than trying to build in a mechanism of herbivore population reduction, which would require estimates of the extent of reduction for each species.

The model monitored the available biomass of food for each herbivore over a period of two years with an increase in numbers of one herbivore. The biomass of the main vegetation types was also monitored, as was the biomass of food eaten each day.

The main results can be summarised as follows:

1. **Bushbuck increased by 10%:**

When this was modelled the available food for the bushbuck, duiker and buffalo dropped much faster than that of the gorillas (see Figure 6.2). This was due mainly to a drop in the availability of grasses and small herbs (Figure 6.3). During this two year period the population size of the herbivores was effectively dropping, however, as certain food-plant species became extinct. Figure 6.4 shows the drop in the proportional intake of food by each herbivore over the same time.

2. **Buffalo increased by 20%:**

Again the availability of bushbuck, duiker and buffalo food dropped more quickly than that of gorilla food (Figure 6.5) and this was again due to a drop in the availability of short herbs and grasses (Figure 6.6). The drop in the proportional intake of food shown in Figure 6.7 gives a similar picture to that of the bushbuck increase.

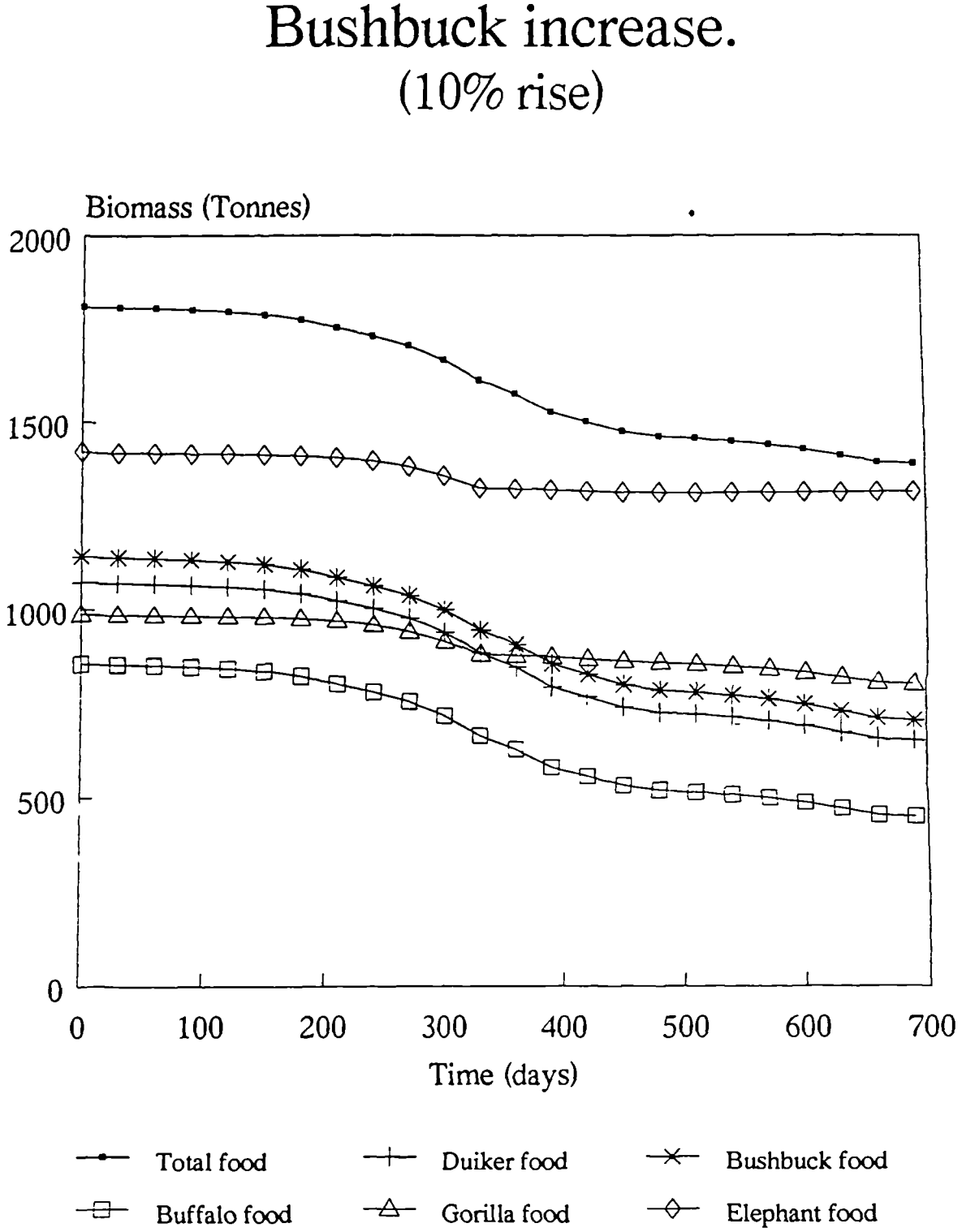


Figure 6.2 The effect of an increase by 10% of the bushbuck population on the food supply of each herbivore species and the total food supply. It was assumed that the current population levels were stable so that an increase in one population must cause a decline in the food supply.

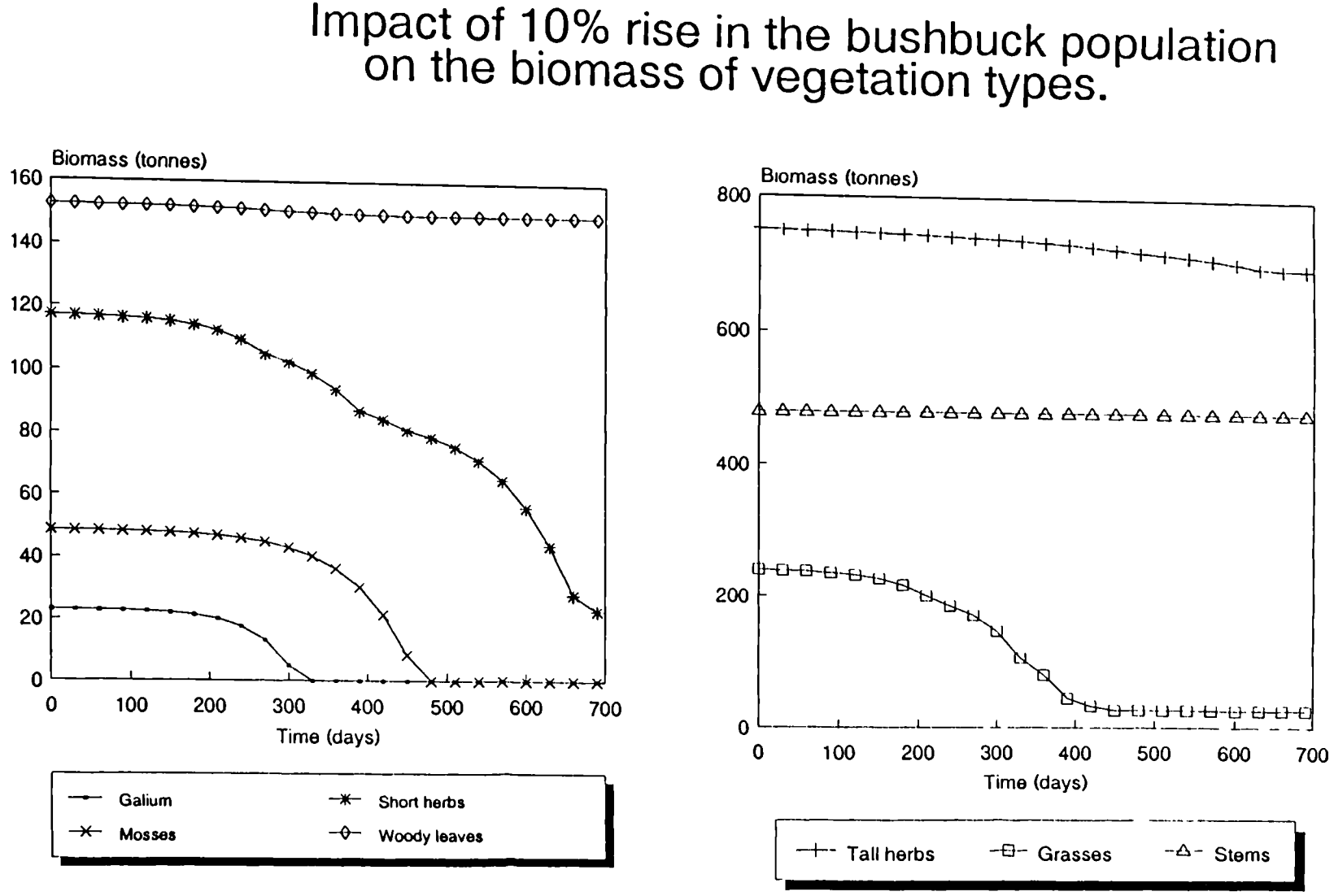


Figure 6.3 The effect of a 10% increase in the bushbuck population on the main plant types in the study area showing that grasses, short herbs and mosses were affected most.

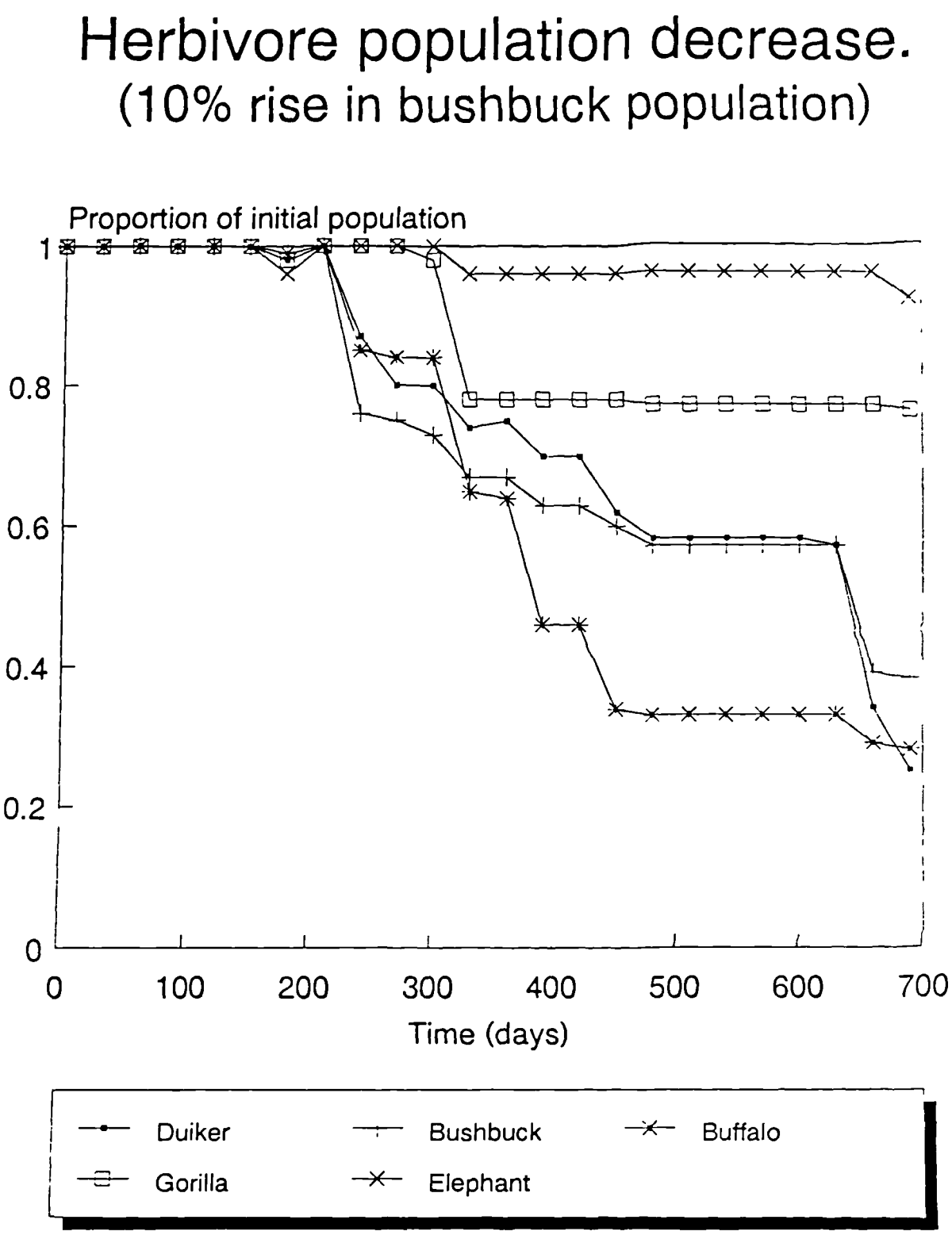


Figure 6.4 The proportional decrease in the population of each herbivore species over the same time period as the previous two figures with a 10% increase in the bushbuck population. The population of a species decreased as certain foods became extinct because dietary switching was not built into the model.

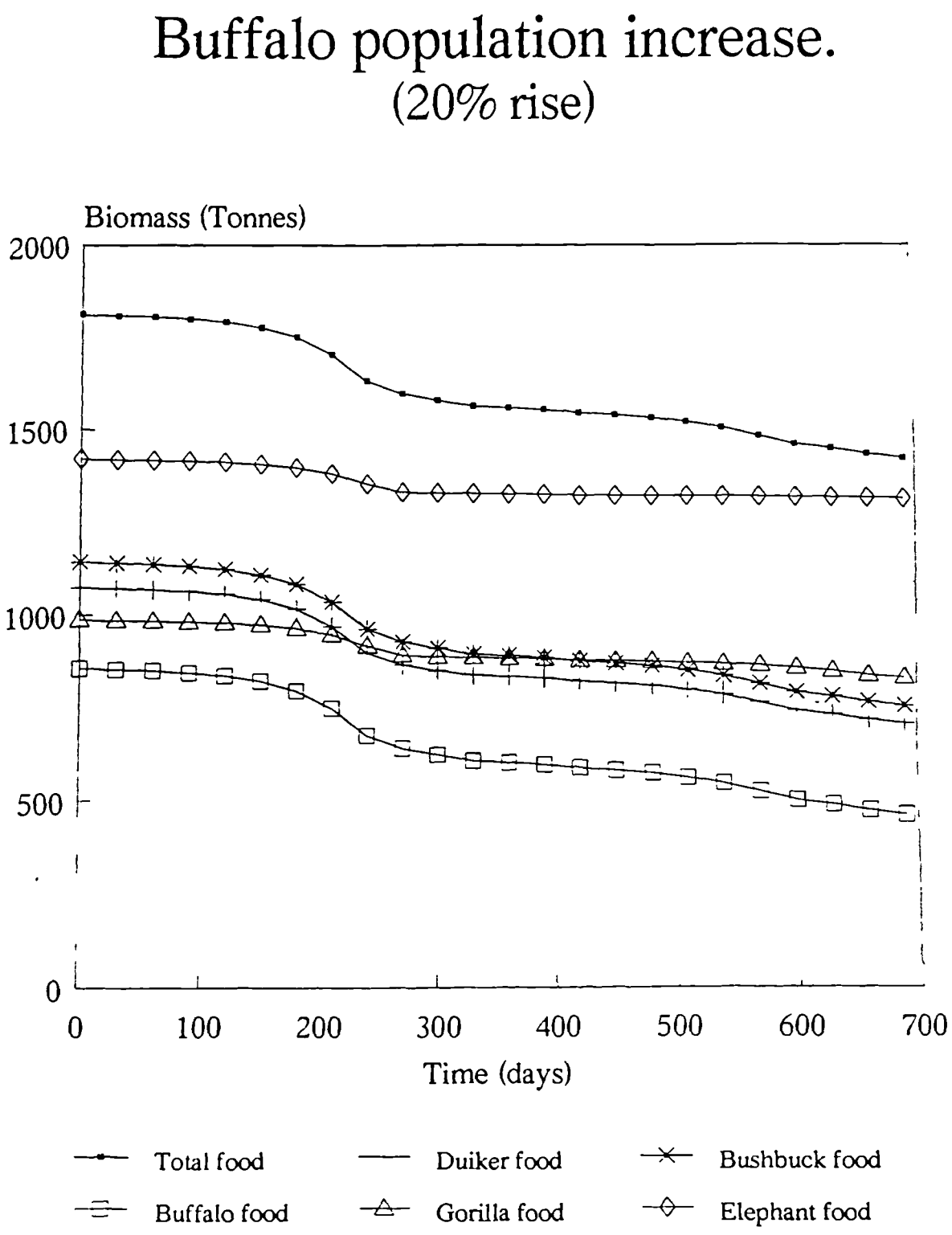


Figure 6.5 The effect of an increase by 20% of the buffalo population on the food supply of each herbivore species and the total food supply. It was assumed that the current population levels were stable so that an increase in one population must cause a decline in the food supply.

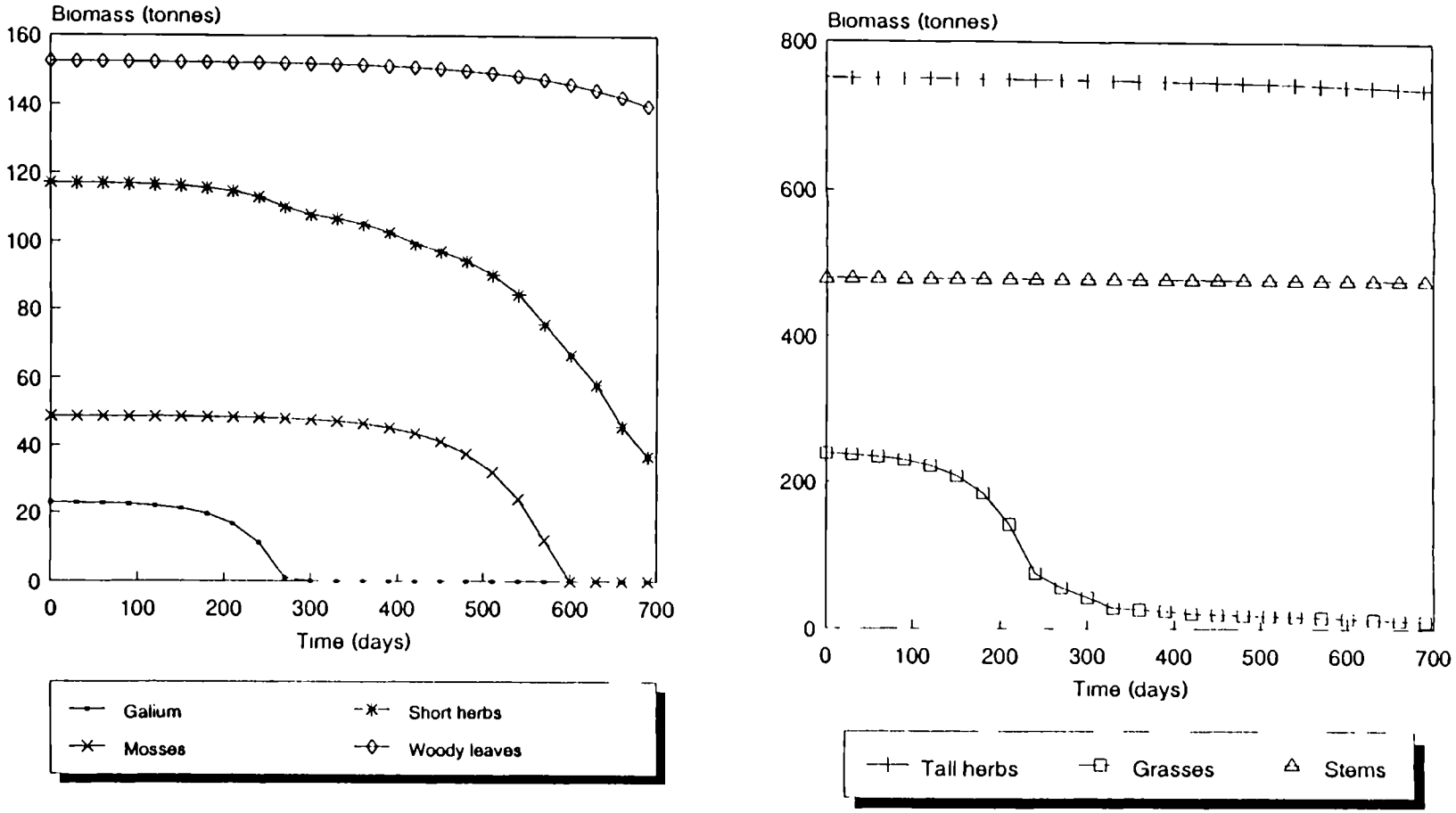


Figure 6.6 The effect of a 20% increase in the buffalo population on the main plant types in the study area showing that grasses and short herbs were affected most.

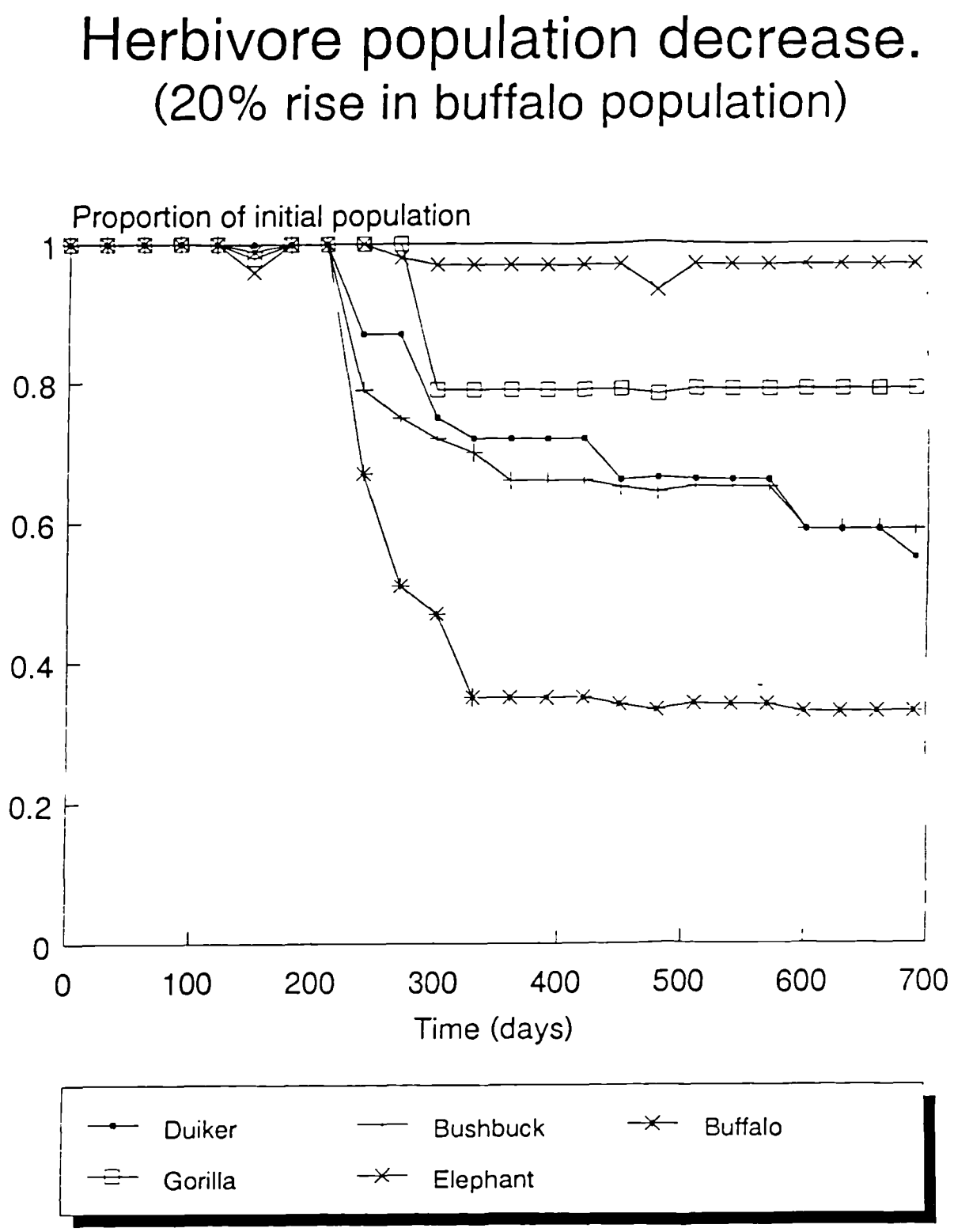


Figure 6.7 The proportional decrease in the population of each herbivore species over the same time period as the previous two figures with a 20% increase in the buffalo population. The population of a species decreased as certain foods became extinct because dietary switching was not built into the model.

3. **Elephants increased by 700%:**

If the seven elephants that visited the study area in 1988 were to remain in this region then the food availability might drop as in Figure 6.8. Over the two years the elephant food availability dropped by more than the gorilla food availability, although initially this was reversed. The woody herbs and the tall herbs contributed to most of this decrease (Figure 6.9). Examination of the decrease in the proportional intake however, showed that the gorilla population was one of the first to show a large decline (Figure 6.10). This was because the *Galium,* which forms a high percentage of their diet (Chapter 4), became extinct and switching by these animals to another food supply was not built into the model.

4. **Gorillas increased by 100%:**

If the gorilla population doubled, then over two years they could have a stronger impact upon other species than they do on themselves (Figure 6.11). This was again due to a decrease in the availability of woody plants tall herbs and also short herbs (which included other vines) (Figure 6.12). Examination of the proportional decrease in intake (Figure 6.13) shows that initially the gorilla population experienced a sharp decline as *Galium* became extinct, after which the duiker and buffalo population showed a decrease and as in Figure 6.11 the level of intake for the duikers dropped below that for the gorillas. This is due to the fact that the gorillas flatten a lot of vegetation eaten by these other species.

In all the runs *Galium* became extinct at some point. It might be that the figure of 70% *Galium* flattening damage was too high and that this might have affected the results, although varying this figure to 20% showed little change in the overall result. As *Galium* formed a major item in the mountain gorillas diet this is quite important. It could be that the measure of productivity for this species was unusually low, although this was unlikely because it was obtained from the growth of small shoots which were

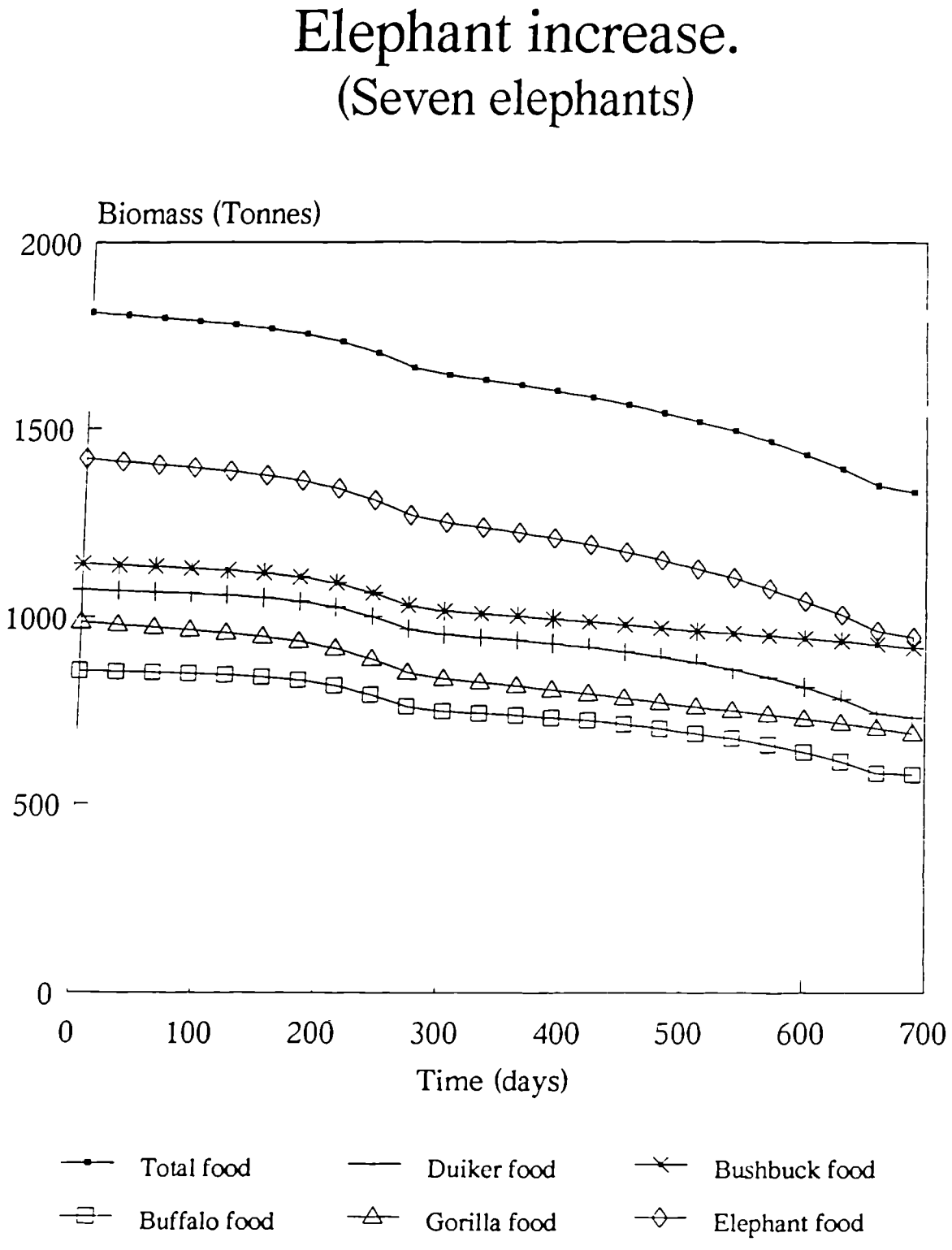


Figure 6.8 The effect of an increase by 700% of the elephant population on the food supply of each herbivore species and the total food supply. It was assumed that the current population levels are stable so that an increase in one population must cause a decline in the food supply. This models the potential effect of the group of seven elephant on the study area if they were to remain there throughout the year.

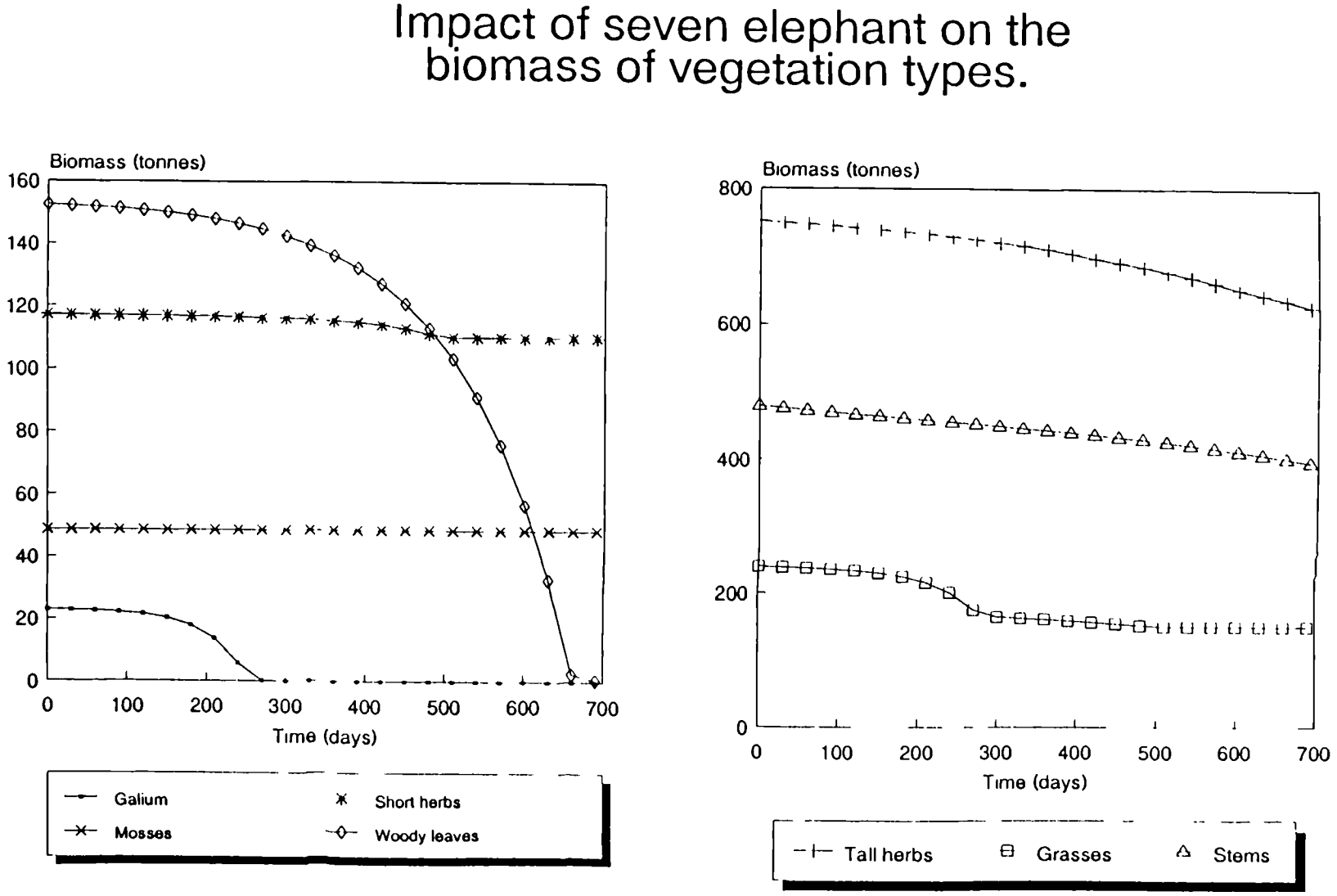


Figure 6.9 The effect of a 700% increase in the elephant population on the main plant types in the study area showing that woody leaves and tall herbs were affected most.

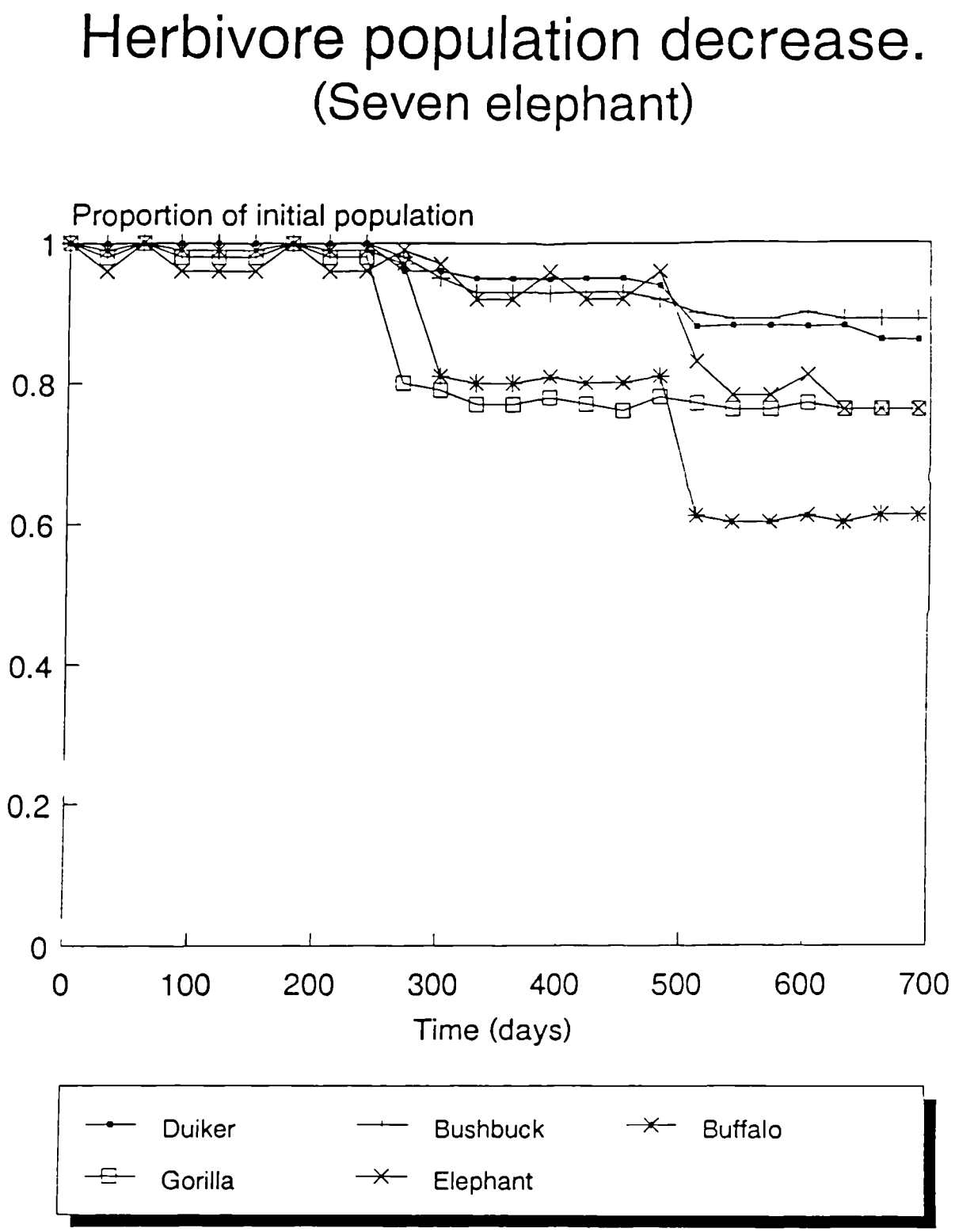


Figure 6.10 The proportional decrease in the population of each herbivore species over the same time period as the previous two figures with a 700% increase in the elephant population. The population of a species decreased as certain foods became extinct because dietary switching was not built into the model.

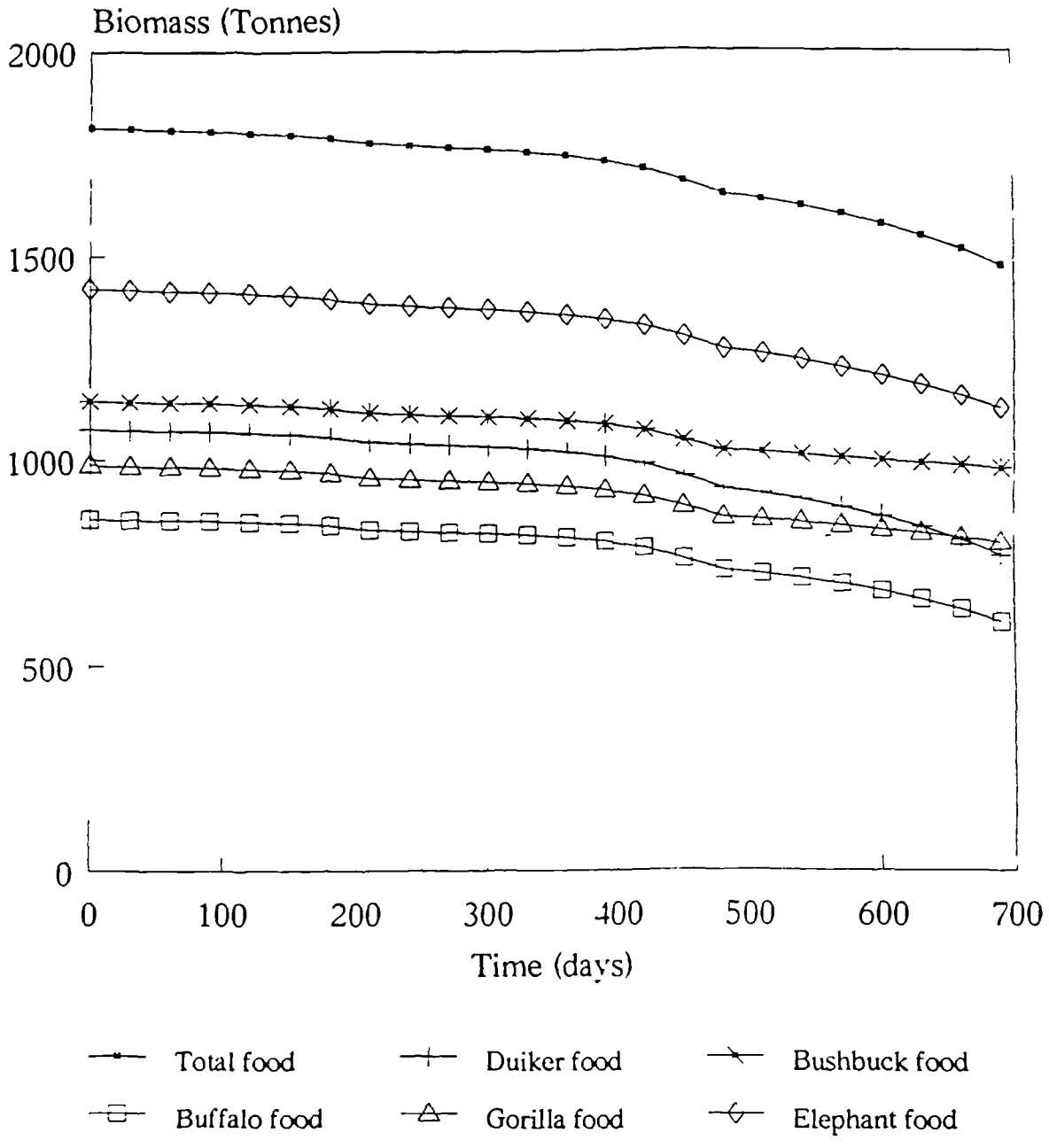


Figure 6.11 The effect of an increase by 100% of the gorilla population on the food supply of each herbivore species and the total food supply. It was assumed that the current population levels were stable so that an increase in one population must cause a decline in the food supply.

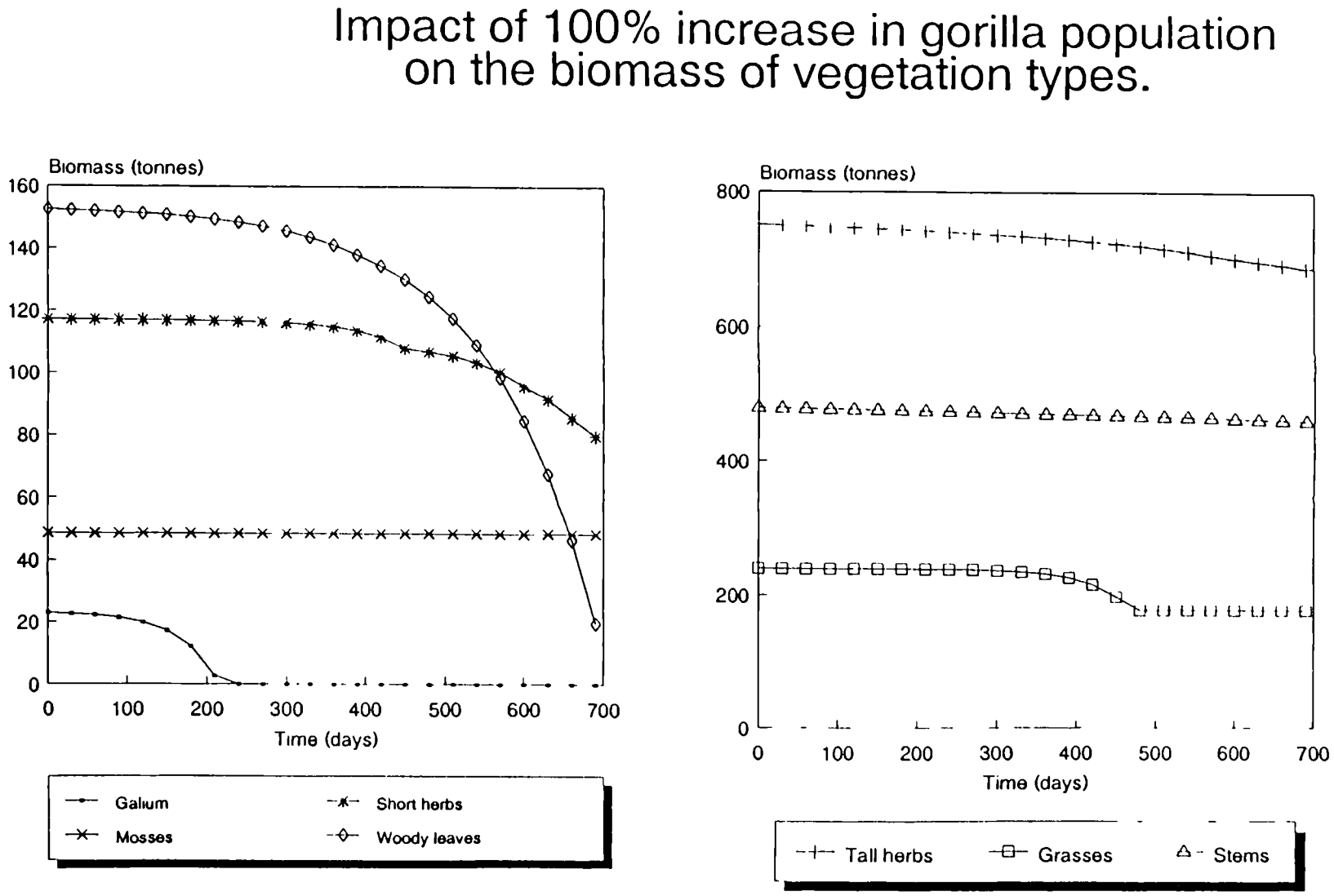


Figure 6.12 The effect of a 100% increase in the gorilla population on the main plant types in the study area showing that woody leaves and tall herbs were affected most.

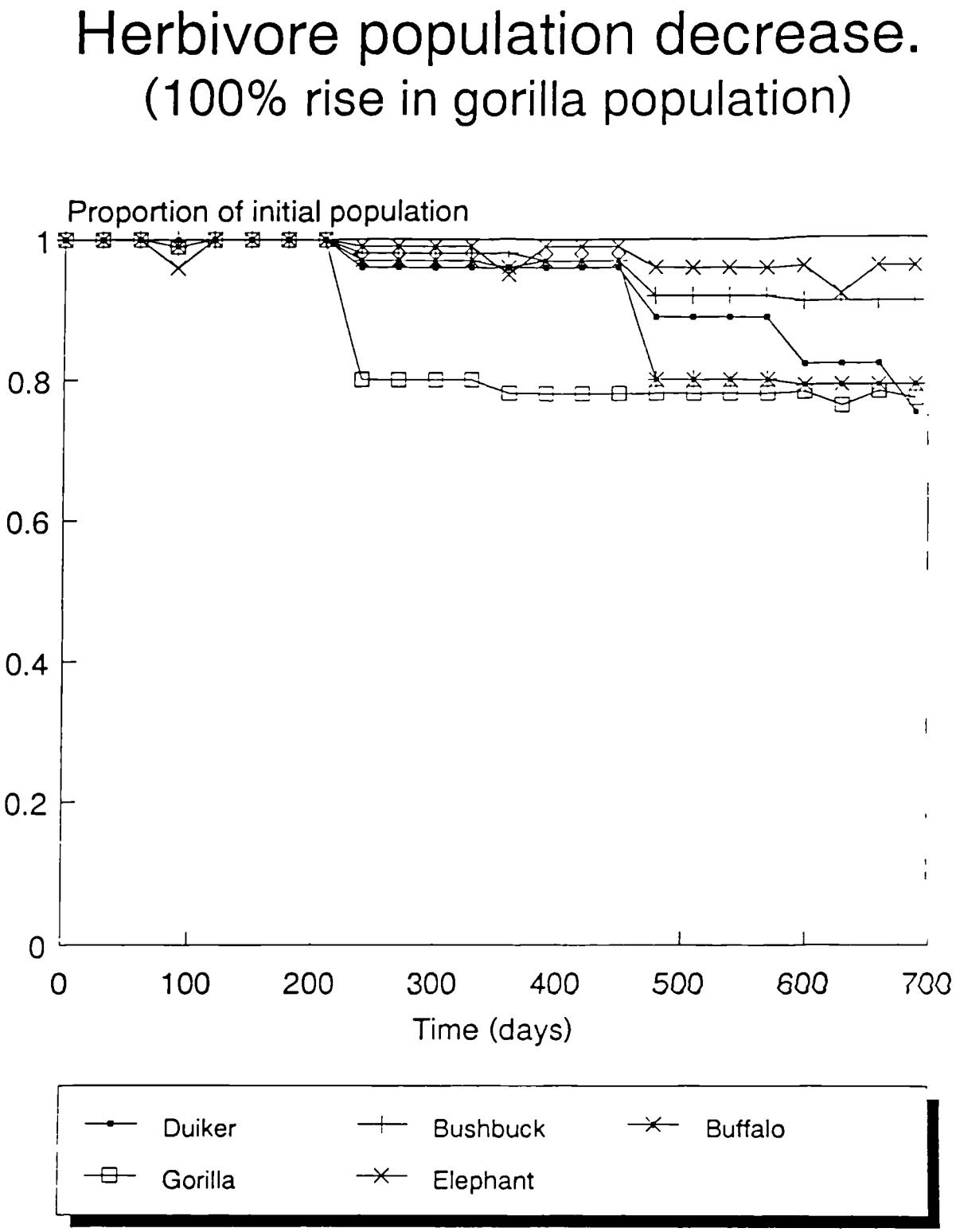


Figure 6.13 The proportional decrease in the population of each herbivore species over the same time period as the previous two figures with a 100% increase in the gorilla population. The population of a species decreased as certain foods became extinct because dietary switching was not built into the model.

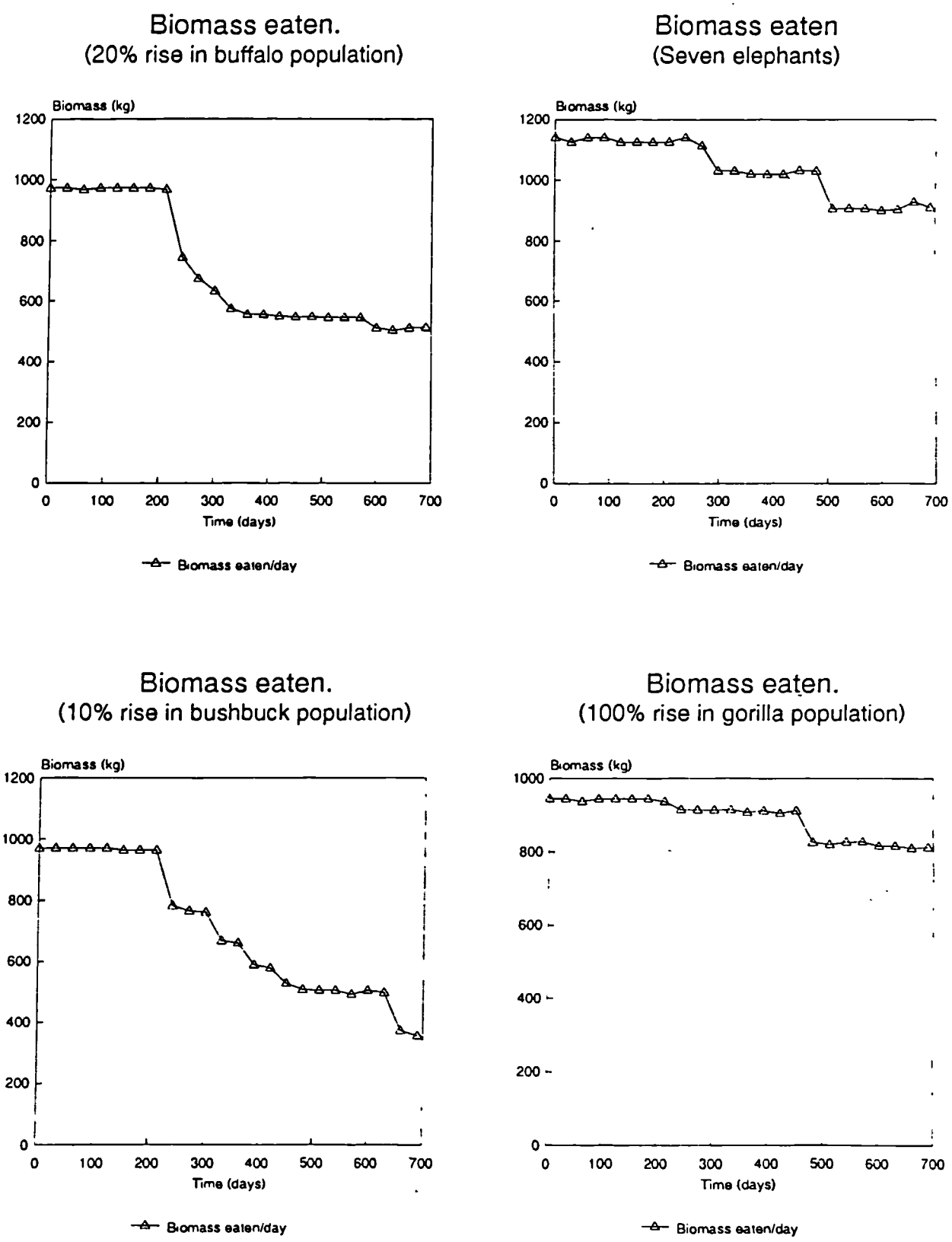


Figure 6.14 The decrease in total biomass intake by all herbivores in the study area with each of the herbivore increases shown previously. This showed that there was a much quicker crash with an increase in the bushbuck or buffalo populations despite a similar initial biomass intake for each run.

more likely to be growing faster than the larger, older clumps of this vine. It is more likely that the value removed as insect/rodent consumption and plant senescence may have been too high or that it was reduced as more of the vine was eaten. The measure that Watts (1983) obtained for gorilla consumption of this species in 1979 was higher than that found in this study (even if the dry mass intake is calculated using the water content figures he gave). This may mean that the *Galium* available to the gorillas has already been reduced as the population has increased over the intervening ten years.

If the amount of vegetation consumed by all these herbivores is examined (Figure 6.14) it can be seen that the buffalo and bushbuck increases show a much quicker crash in overall consumption than the elephant and gorilla increases, despite similar initial consumption rates. Examination of Figures 6.4 and 6.7 shows that this is mainly due to a crash in the intake of the bushbuck, buffalo and duiker in both cases. This is partly explained by the fact that the growth of the tall herbs was described by a curve function rather than a step function, as was used for the small herbs and grasses. Sensitivity analysis of the model parameters, however, showed that varying the mass at which the growth of the small herbs was doubled had little effect on this result. Thus the short herbs and grasses were more likely to become rare with an increase in consumption, implying that they were being heavily used. The tall herbs utilised by the gorillas and elephant seemed to have a greater capacity to compensate for an increase in the herbivore pressure. This indicated that the bushbuck and buffalo populations were probably nearer to the ecological carrying capacity of the ecosystem than the elephant and gorillas. This is reasonable as these latter two species have a much slower reproductive rate and so would be less likely to have increased to a maximum population size in the twenty years they have been protected.

Sensitivity analysis of various parts of the model showed little change in these results except in the time scale over which they occurred. It would be possible to make this model more complex using dynamic rather than static modelling, but this would

require assumptions for which there are no data for the Birungas. For instance it would be possible to incorporate growth rates of the animal populations and some method of dietary switching, but should this be done it would become increasingly difficult to accept the results obtained. The model as it stands answers the basic question about the probable impact of increases in these herbivores on the gorilla population. In all cases, the food supply of the other herbivores was affected to a greater extent over a long period of time and the populations of the other herbivores crashed before the gorilla population.

6.4. Conclusion

Much more work will be required to fully understand the plant-herbivore dynamics in the Birungas. This ecosystem holds a comparatively high mammalian herbivore biomass compared with other forest ecosystems and it is probable that at least the buffalo and bushbuck are at or near their ecological carrying capacity. If food does limit these animals then "exploitative" or "consumptive" competition would be expected to occur (Schoener 1983). The results of the niche overlap study strongly indicated that competition had caused a hyperdispersion of the dietary niches of these herbivores. Furthermore the herbivores were constrained to utilise the habitats at lower altitudes, thereby increasing the potential for competition between the species.

If the vegetation was assumed to have been at a stable level and the herbivore numbers varied it was found that, despite the low dietary overlap, competition could still occur because the food supplies of all species were reduced. However, the results showed that intraspecific competition for food by most of the herbivores will be much stronger than interspecific competition. The drop in total biomass of food eaten with time (Figure 6.14) showed that both the buffalo and bushbuck were more likely to be food limited than the elephant and gorillas, because many of their food species

become rare quickly. This was not surprising as these two herbivores form by far the dominant biomass in the study area.

The mountain gorilla population therefore would seem to be capable of some continued expansion without any significant consequences to the ecosystem and their numbers do not seem to be strongly affected by the other herbivores. Whilst the elephant population would be the most likely to have an impact upon the gorillas, their numbers were very small in the reserve and hence are unlikely to prove a problem.

CHAPTER SEVEN

MANAGEMENT IMPLICATIONS

This study has shown that the mountain gorilla population is unlikely to be affected by changes in the numbers of the other large herbivores in the Birungas. It is most likely in fact that the gorillas themselves have a detrimental effect upon the other herbivores. It is not necessary therefore to instigate any form of culling program of the antelope or buffalo to conserve the habitat for the gorillas.

However, so far, all these data are based on an area of only $12km^2$ (about 3% of the reserve) around Karisoke, and they may not apply to all other areas. It is suggested therefore, that this work is extended to the rest of the park, particularly the censusing of each herbivore species at regular intervals to identify changes in the animal populations. This could most easily be done using clearance plots in known locations rather than transect counts, since they are quick to census and results are obtained easily. Even if the counts are not actual counts of the herbivores because the vegetation is opened up or the plots are not randomly placed, they could usefully show if a population was increasing or decreasing. A similar project could be set up to monitor vegetation plots over a long time period in order to see whether the vegetation is changing in any way. Certainly the paucity of *Vernonia* trees (pers. obs.) compared with Watts (1983) indicates that the gorillas (which feed on the flowers and pith, breaking up the tree in the process) have probably had a detrimental effect on this species.

Due to the time constraints of this project, the model described in Chapter 6 had to make a number of assumptions, and further work would allow it to be refined. No measure of plant competition or use of the soil nutrients was built into the model. The

model also assumed that the herbivores utilised a habitat evenly and yet the study of dung deposition within habitats showed this was not the case. The patchiness of plant distributions within a habitat (Chapter 2) also made it unlikely that the herbivores would use the habitat evenly. This uneven use however, would make it less likely that the gorillas would be affected by the other herbivores unless they selectively used the same patches. This was not the case as the niche overlap by the herbivores was reduced (except for gorillas and elephant) when the use of vegetation types within habitats was included (Table 6.4). Sensitivity analysis on the model did not alter the main findings however, and therefore the model was relatively robust. This meant that the results produced by the model were more likely to reflect reality.

The ability of the herbivores to switch their diet and concentrate on other food plants is the main factor that might alter the results of the model. Unfortunately no data exist to allow predictions as to how this might occur. Walker (1979) argued that dietary niche overlap between species is usually quite high, which allows flexibility in the choice of food-plant species by the animals and can allow switching to occur. Here, however, dietary niche overlap is low which may mean that the flexibility is lowered through past or present competitive interactions.

In this study gorilla diet was also analysed in other areas of the park. Faeces were collected during the 1989 mountain gorilla census and combined into three other zones; the Sabinyo-Muhabura sector in the east, the Visoke-Sabinyo sector to the north of Karisoke, and the Mikeno region in the west. The results are given in Figure 7.1, showing that there was a difference in the proportions of plant parts in the diet. Bamboo leaves were particularly important elsewhere in the park where bamboo was available to these animals. This species therefore has quite a degree of flexibility in the relative intake of its food-plant species and seems to be able to alter its diet quite easily.

Gorilla diet.

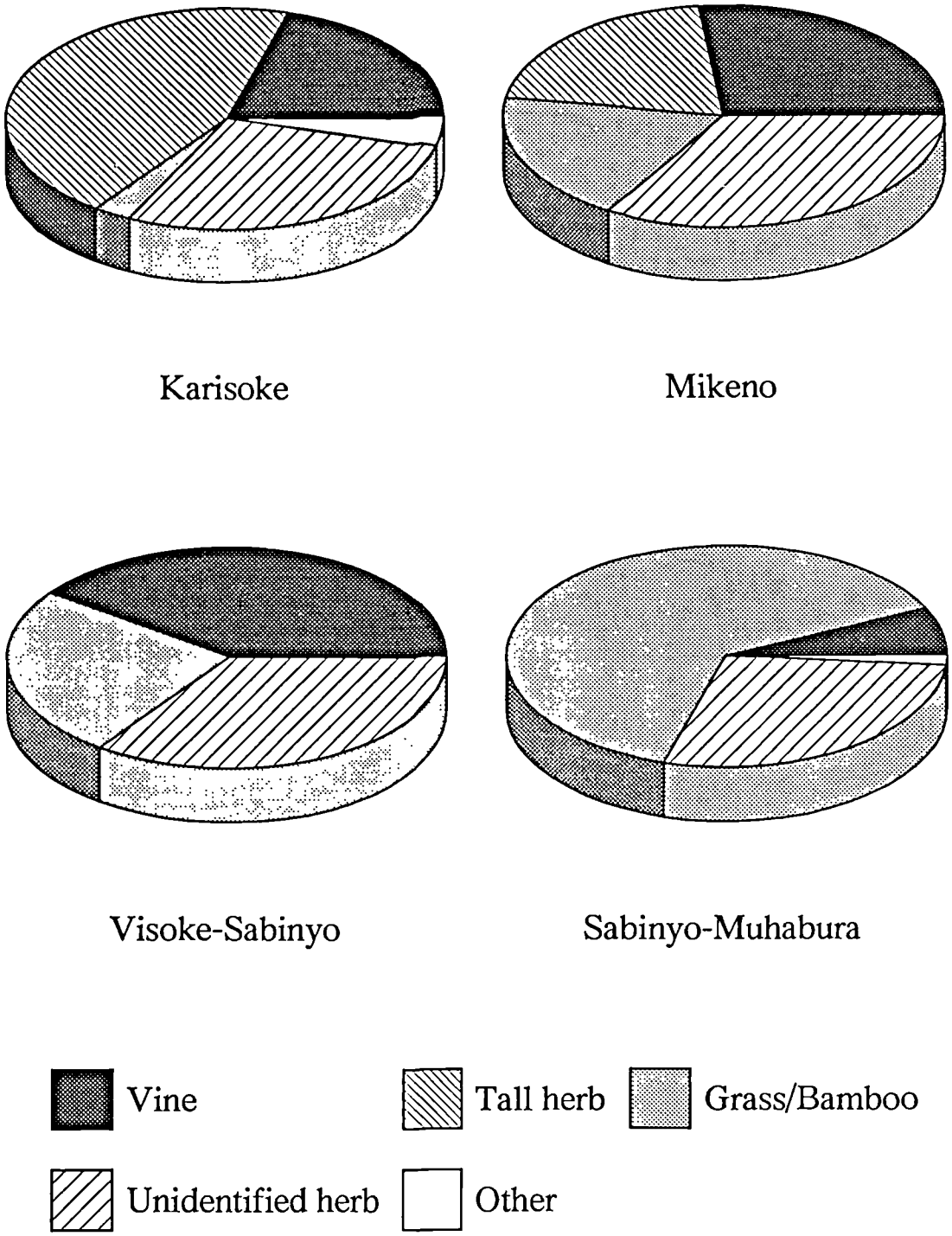


Figure 7.1 The proportional biomass intake of food-plant types by gorillas in various regions of the Parc National des Volcans. Data were collected using microhistological analysis of faecal material collected during the 1989 mountain gorilla census.

To expand and improve the model a study of the population dynamics of each herbivore species is needed to identify the factors that are limiting the populations, if they are indeed limited. It could be that certain nutrients that have not been measured may be in short supply in certain food-plants or that there are some allelochemicals present. Energy could well be limiting the populations, as has been found elsewhere (Owen-Smith & Cooper 1989), or climatological factors may be important. The only species which I have identified where food is probably limiting is the buffalo population, because the density of the sward is lower than that required to maintain body condition in most habitat types (see Chapter 4). This may be one reason why these animals are frequently leaving the park at night in search of food.

The results of the niche overlap study indicated that the animals were constrained to use the lower altitude habitats in the park. This supports the suggestion that some of these species have been forced up higher through habitat loss at lower altitudes. Hence any more deforestation would be highly detrimental and if the possibility arises land should be repurchased to allow reafforestation at lower altitudes. The corridor that exists between the Virunga savanna park in Zaire and the volcanos should also be protected to allow the access of elephants to the park. This is necessary if this population is to survive as it is unlikely that the small size of the park can support a viable population of these animals. Elephants, whilst having the greatest niche overlap with the gorillas, may also have beneficial effects such as opening-up the vegetation, thereby allowing the growth of the herbaceous plants favoured by the gorillas. Detailed monitoring of plant population dynamics would confirm whether this is the case.

In conclusion, the future of the mountain gorilla in the Birungas is relatively secure. Interspecific competition between the other herbivores and the gorillas will not affect this endangered species greatly, and is more likely to have a detrimental impact on the populations of these other species. This species also appears to be relatively flexible

in its dietary requirements despite the finding by Watts (1983) and this study that only a few plant species form the bulk of their diet around Karisoke. Measurements of the productivity of these food-plants showed that it is probable that they can accommodate an increase in the gorilla population even around Karisoke, where the density of gorillas is probably the highest for any region of the reserve. Soulé *et al.* (1979) argued that a reserve such as the Birungas will always require active management in order to maintain the plant and animal species diversity. Therefore it is strongly suggested that long term monitoring programs are instigated to regularly census the large herbivores and to investigate any long term changes in the vegetation. Programs such as these would identify changes detrimental to the gorillas before it is too late, and would provide data which will allow management decisions to be made and tested before they are fully implemented.

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APPENDIX 1:

Plant species found in the study area. Species were identified using herbarium material and Troupin's Flora of Rwanda (**Troupin G. (1978-1988)** *Flora du Rwanda: spermatophytes vols.I-IV*).

Moss:
Selaginella kraussiana (Kunze) A. Braun.

Acanthaceae:
Mimulopsis excellens Lindau.

Apiaceae:
Hydroctyle mannii Hook f.
Hydroctyle ranunculoides L.f.
Hydroctyle sibthorpioides Lam.
Oenanthe procumbens (H.Wolff).Norman.
Peucedanum kerstenii Engl.
Peucedanum linderi Norman

Asclepiadaceae:
Tylophoropsis heterophylla N.E.Br.

Asteraceae:
Carduus kikuyorum R.E.Fries.
Carduus nyassanus (S.Moore) R.E.Fries.
Cineraria kilimandscharica Engl.
Conyza adolfi-fridericii (Muschler) Wild.
Crassocephalum ducis-aprutii (Chiov.) S.Moore.
Crassocephalum mannii (Hook f.) Milne-Redh.
Gynura ruwenzoriensis (S.Moore) S.Moore.
Helichrysum formosissimum (Schultz-Bip) ex.A.Rich.
Helichrysum globosum Schultz-Bip ex A.Rich.
Prenanthes subpeltata Stebbins.
Senecio johnstonii Oliver.
Senecio maranguensis O.Hoffm.
Senecio mariettae Muschler.
Senecio sabinjoensis Muschler.
Senecio transmarinus S.Moore.
Senecio trichopterygius Muschler.
Vernonia adolfi-fredericii Muschler.
Volkensia ruwenzoriensis (S.Moore) B.L.Burtt.

Balsaminaceae:
Impatiens (L.) *burtonii* Hook f.
Impatiens stuhlmannii Warb.

Campanulaceae:
Lobelia giberroa Hemsley.
Lobelia mildbraedii
Lobelia stuhlmannii Schweinf. ex Stuhlmann.
Lobelia wollastonii Baker f.

Caryophyllaceae:
Cerastium indicum Wight & Arn.
Cerastium octandrum Hochst. ex A.Rich.
Stellaria sennii Chiov.

Clusiaceae:
Hypericum peplidifolium A.Rich.
Hypericum revolutum Vahl.

Cruciferae:
Cardamine obliqua Hochst. ex A. Rich.

Cucurbitaceae:
Zehneria scabra (L.f.) Sonder.

Cyperaceae:
Carex bequaertii De Wild.
Carex erythrorhiza Boeckler var scabrida kuek.
Carex simensis A.Rich.
Cyperus dichroostachyus Hochst. ex A.Rich.
Isolepis costata Hochst. ex A.Rich.
Isolepis setaceae (L.) R.Br.
Mariscus karisimbiensis Chermezon.

Ericaceae:
Philipia johnstonii Engl.

Gentianaceae:
Swertia macrosepala Gilg.

Geraniaceae:
Geranium arabicum Forsskal.
Geranium aculeolatum Oliver.

Juncaceae:
Juncus dregeanus Kunth.
Luzula abyssinica Parl.
Luzula johnstonii Buchenau.

Lamiaceae:
Mentha aquatica L.
Plectranthus sylvestris Guerke.
Pychnostachys goetzenii Guerke.
Solenostemon sylvaticum (Guerke) Agnew.
Stachys aculeolata Hook.f.

Leguminosae:
Parochetus communis Buch.-Ham. ex D.Don.
Trifolium tembense Fresen.
Trifolium usambarense Taubert.

Loranthaceae:
Englerina woodfordioides (Schweinf.) Balle.

Menispermaceae:
Stephania abyssinica (Dill. ex Rich. Walp.

Orchidaceae:
Disa stairsii Kraenzlin.

Oxalidaceae:
Oxalis procumbens Steudel ex A.Rich.

Poaceae:
Arundinaria alpina Schumann.
Agrostis kilimandscharica Mez.
Agrostis quinqueseta (Steudel) Hochst.
Agrostis schimperiana Steudel.
Agrostis taylori C.E.Hubb.
Bromus leptocladus Nees.
Festuca engleri Pilg.
Festuca schimperiana A.Rich.
Panicum striatissimum Hubb.
Poa annua L.
Poa schimperana A.Rich.

Polygonaceae:
Polygonum nepalense Meissn.
Rumex bequaertii De Wild.
Rumex ruwenzoriensis Chiov.

Ranunculaceae:
Ranunculus bequaertii De Wild.
Ranunculas multifidus Forsk.
Ranunculus volkensii Engl.

Rosaceae:
Alchemilla cryptantha A.Rich.
Alchemilla johnstonii Oliv.
Alchemilla kiwuensis Engl.
Hagenia abyssinica (Bruce) J.F.Gmel.
Rubus kirungensis Engl.
Rubus runssorensis Engl.

Rubiaceae:
Galium chloroionanthum Schumann.
Galium ruwenzoriense (Cortesi) Chiov.

Solanaceae:
Solanum aculeastrum Dunal.
Solanum anguivii Lam.
Solanum nigrum L.

Sterculiaceae:
Dombeya goetzenii Schumann.

Urticaceae:
Droquetia iners (Forsk.) Schweinf.
Girardinia bullosa (Hochst. ex Steud.) Wedd.
Laportea alatipes Hook.f.
Parietaria debilis Forst.
Pilea rivularis Wedd.
Urtica massaica Mildbr.

APPENDIX 2.

Equations relating plant height in centimetres to dry mass in grams. The number of samples (n), regression coefficient (r) and the significance of the fit are given below each equation (Plant height was measured from the meristem at the apex of the plant to the ground. Stem diameter was measured at ground level. Leaf length was from the leaf tip to the base of the petiole where it met the stem)

Species:

Crassocephalum ducis-aprutii:

Total mass: $\mathbf{mass} = 6.63 \times 10^{-3} * (\mathbf{height})^{1.661}$
(n=44, r=0.97, P<0.001)

Leaf mass: $\mathbf{mass} = (0.035 * \mathbf{height}) - 0.179$
(n=44, r=0.89, P<0.001)

Solenostemon sylvaticum:

Total mass: $\mathbf{mass} = 0.0145 * (\mathbf{height})^{1.282}$
(n=44, r=0.97, P<0.001)

Leaf mass: $\mathbf{mass} = (0.017 * \mathbf{height}) - 0.033$
(n=45, r=0.88, P<0.001)

Urtica massaica:

Total mass: $\mathbf{mass} = 7.11 \times 10^{-3} * (\mathbf{height})^{1.589}$
(n=53, r=0.98, P<0.001)

Leaf mass: $\mathbf{mass} = (0.048 * \mathbf{height}) - 0.471$
(n=52, r=0.87, P<0.001)

Stachys aculeolata:

Total mass: $\mathbf{mass} = 7.03 \times 10^{-3} * (\mathbf{height})^{1.216}$
(n=40, r=0.97, P<0.001)

Leaf mass: $\mathbf{mass} = (0.0068 * \mathbf{height}) + 0.016$
(n=40, r=0.94, P<0.001)

Galium spp.:

Total mass: $\mathbf{mass} = 1.06 \times 10^{-3} * (\mathbf{height})^{1.483}$
(n=55, r=0.96, P<0.001)

Carex simensis:

Leaf mass: $\mathbf{mass} = 6.26 \times 10^{-4} * (\mathbf{leaf\ length})^{1.396}$
(n=89, r=0.99, P<0.001)

Carex bequaertii:

Leaf mass: $\mathbf{mass} = 6.9 \times 10^{-4} * (\mathbf{leaf\ length})^{1.591}$
(n=38, r=0.95, P<0.001)

Peucedanum kerstenii:

Leaf mass: $\mathbf{mass} = 1.57 \times 10^{-3} * (\mathbf{leaf\ length})^{1.710}$
(n=31, r=0.98, P<0.001)

Echinops hoehlenii:

Leaf mass: $\mathbf{mass} = 4.7 \times 10^{-4} * (\mathbf{leaf\ length})^{2.262}$
(n=19, r=0.95, P<0.001)

Helichrysum globosum:

Leaf mass: $\mathbf{mass} = (0.0148 * \mathbf{height}) - 0.038$
(n=33, r=0.82, P<0.001)

Rubus spp.:

Leaf mass: **mass** = (0.2114***stem length**)-4.852
(n=26, r=0.94, P<0.001)

Hypericum revolutum:

Leaf mass: **mass** = (0.0610***stem length**)-0.707
(n=40, r=0.79, P<0.001)

Laportea alatipes:

Total mass:0-76cm: **mass** = 0.04128*(**height**)$^{1.149}$
(n=23, r=0.95, P<0.001)

77cm+ : **mass** = (0.3396***height**)-19.93
(n=22, r=0.89, P<0.001)

Leaf mass: **mass** = 0.0571*(**height**)$^{0.845}$
(n=43, r=0.90, P<0.001)

Carduus nyassanus:

Stem mass: **mass** = 8.86x10^{-3}*(**height**)$^{1.581}$
(n=29, r=0.98, P<0.001)

Leaf mass:0-36cm **mass** = 6.06x10^{-3}*(**leaf length**)$^{1.618}$
(n=45, r=0.98, P<0.001)

77cm+ **mass** = (0.1021***leaf length**)-2.00
(n=27, r=0.94, P<0.001)

Impatiens spp.:

Total mass:0-51cm **mass** = 6.16x10^{-3}*(**height**)$^{1.388}$
(n=50, r=0.96, P<0.001)

52cm+ **mass** = (0.051***height**)-1.163
(n=17, r=0.86, P<0.001)

Leaf mass: **mass** = (0.009***height**)-0.032
(n=48, r=0.94, P<0.001)

Peucedanum linderi:

Stem mass:0-234 **mass** =0.0606*(**height*stem diameter**)$^{1.107}$
(n=29, r=0.95, P<0.001)

235+ **mass** =(0.147***height*stem diameter**)-10.132
(n=13, r=0.95, P<0.001)

Leaf mass:0-43cm **mass** = 1.66x10^{-3}*(**leaf length**)$^{1.841}$
(n=41, r=0.93, P<0.001)

44cm+ **mass** = (0.121***leaf length**)-3.680
(n=22, r=0.87, P<0.001)

Plectranthus sylvestris:

Total mass:0-87cm **mass** = 2.45x10^{-3}*(**height**)$^{1.726}$
(n=31, r=0.98, P<0.001)

88cm+ **mass** = (0.205***height**)-12.478
(n=20, r=0.93, P<0.001)

Leaf mass: 0-89cm **mass** = 2.64x10^{-3}*(**height**)$^{1.402}$
(n=49, r=0.97, P<0.001)

90cm+ **mass** = (0.032***height**)-1.420
(n=21, r=0.86, P<0.001)

APPENDIX 3

The total biomass (Tonnes) of each species of plant in each habitat in the study area. This was determined from the product of the mean biomass per square metre and the area of each habitat type given in Chapter 2. Standard errors are given after each figure.

SPECIES		BAMBOO	SADDLE	MEADOW	HERBACEOUS
Woody plants:					
Lobelia giberroa lvs.		0.669±0.414	86.727±9.621		42.918±5.470
Rubus spp.			0.289±0.186		0.983±0.983
Hypericum revolutum lvs.			0.559±0.161	0.003±0.003	
Tall herbs:					
Crassocephalum	Total	2.625±0.625	408.979±38.254		389.523±41.076
ducis-aprutii	Leaf	0.834±0.203	103.593±9.107		86.464±7.992
Laportea alatipes	Total	4.264±1.165	370.107±35.921		130.860±15.499
	Leaf	1.376±0.356	105.572±9.210		33.432±4.076
Urtica massaica	Total	0.027±0.027	24.037±8.323		18.577±6.600
	Leaf	0.015±0.015	9.460±3.400		7.129±2.546
Senecio	Total	0.040±0.040	1.562±1.446		0.315±0.315
transmarinus	Leaf	0.010±0.010	0.450±0.405		0.089±0.089
Peucedanum linderi	Total	0.419±0.118	8.336±3.837		52.981±11.912
	Leaf	0.254±0.124	1.369±0.591		18.855±4.055
Peucedanum kerstenii				1.547±0.273	
Carduus nyassanus	Total	0.011±0.011	126.011±16.621	0.005±0.005	30.578±10.444
	Leaf	0.011±0.011	86.291±11.003	0.005±0.005	21.266±7.500
Echinops hoelenii	Leaf	0.014±0.014			2.487±2.487
Stachys aculeolata	Total	0.019±0.012	2.629±0.501		1.974+0.476
	Leaf	0.007±0.005	1.112±0.206		0.717±0.176
Senecio	Leaf	0.001±0.001	3.021±0.868		0.572±0.572
trichopterygius					
Oenanthe procumbens	Leaf	0.009±0.009	0.225±0.103		2.507±0.861
Solenostemon	Total	7.226±1.871	185.237±22.347		138.928±19.795
sylvaticum	Leaf	2.754±0.682	73.141±8.587		51.012±7.107
Plectranthus spp.	Total		81.303±18.954		38.550±10.633
	Leaf		29.276±5.855		13.916±3.259
Impatiens spp.	Total	1.285±0.334	60.749±9.037		30.017±11.629
	Leaf	0.436±0.107	24.982±3.843		9.964±3.107
Vines:					
Droquetia iners	Leaf	0.008±0.008	0.360±0.096		0.633±0.187
Galium spp.		0.112±0.040	9.075±1.857	0.083±0.024	9.094±1.585
Tylophoropsis sp.		0.029±0.018	0.039±0.039		0.048±0.048
Stephania abyssinica					2.004±0.733
Gynura ruwenzoriensis		0.039±0.027			0.650±0.526
Zehneria scabra			0.090+0.083		0.033±0.022

Appendix 3 (Continued)

Grasses:				
Carex bequaertii	0.038±0.038	5.174±3.721	10.645±2.360	2.722±2.722
Cyperus marii		8.882±7.082		
Carex simensis	0.220±0.166	24.256±7.513	0.103±0.091	1.220±1.220
Carex erythrorhiza		32.406±9.589	14.059±1.919	
Carex johnstonii		5.592±4.473		
Agrostis spp.	0.019±0.014	7.391±1.382	1.313±0.221	0.041±0.041
Poa annua		0.649±0.379		
Deschampsia flexuosa			0.050±0.050	
Festuca schimperiana		0.244±0.231	1.381±0.314	
Festuca engleri		9.036±2.468		0.791±0.598
Panicum striatissimum			1.833±0.745	
Luzula abyssinica		0.090±0.090	0.777±0.214	
Luzula johnstonii				
Mariscus Karisimbiensis		1.832±0.970	0.586±0.357	
Isolepis spp.			1.968+0.515	
Juncus dregeanus			0.073±0.068	
Small herbs:				
Senecio sabinjoensis				
Helichryssum globosum		0.167±0.128	4.775±1.182	
Hydroctyle spp.	0.117±0.052	20.548±1.838	0.379±0.061	1.250±0.350
Parochetus communis	0.028±0.009	3.676±0.514	0.029±0.013	0.071±0.054
Oxalis		0.032±0.026		
Trifolium spp.			0.063±0.046	
Stelleria sennii	0.015±0.011	4.306±0.720	0.006±0.006	0.224±0.187
Pilea rivularis	0.063±0.026	9.191±1.851		3.961±1.246
Alchemilla spp.		11.286±1.710	0.234±0.070	0.202±0.111
Alchemilla johnstonii			0.044±0.031	
Viola emminii	0.024±0.014	4.673±0.842	0.041±0.024	0.111±0.087
Mentha aquatica		0.868±0.289	0.107±0.037	
Ranunculus spp.	0.006±0.006	1.343±0.366	0.041+0.017	
Cerastium spp.	0.148+0.122	0.138±0.069	0.020±0.020	
Hypericum peplidifolium		0.090±0.071	0.862±0.246	
Cardamine obliqua		0.045±0.045	0.066±0.025	0.122±0.122
Rumex bequaertii		0.174±0.102	0.018±0.011	
Rumex ruwenzoriense				0.009±0.009
Geranium arabicum		0.206±0.135	0.082±0.031	
Swertia macrosepala			0.433+0.371	
Polygonum nepalense		0.938±0.372		0.020±0.020
Plantago palmata		0.206±0.096		
Selaginella kraussiana	0.380±0.142	35.279±4.923	0.215±0.090	3.687±1.678
Total mass	17.949	1,559.137	41.981	908.681
Total leaf mass	7.729	725.432	41.981	317.964

Appendix 3 (Continued)

SPECIES		BRUSH RIDGE	GIANT LOBELIA	ALPINE	KARISIMBI MEADOWS
Woody plants:					
Lobelia giberroa lvs.		14.026±2.207			
Rubus spp.		0.125±0.125	0.69±0.36	0.230±0.147	0.030±0.022
Hypericum revolutum lvs.		0.106±0.067	0.320±0.084	0.030±0.030	0.030±0.022
Tall herbs:					
Crassocephalum	Total	36.600±8.006	1.197±0.484	2.112±0.934	15.131±5.902
ducis-aprutii	Leaf	9.049±1.792	0.417±0.146	0.534±0.218	3.591±1.253
Laportea alatipes	Total	23.137±4.331	0.267±0.267		
	Leaf	6.797±1.181	0.078±0.078		
Urtica massaica	Total				
	Leaf				
Senecio	Total		0.535±0.535		
transmarinus	Leaf		0.149±0.149		
Peucedanum linderi	Total	0.903±0.522			
	Leaf	0.319±0.187			
Peucedanum kerstenii		0.014±0.013	1.891±0.383		
Carduus nyassanus	Total	24.497±3.986	10.734±2.214	0.300±0.294	5.034±2.116
	Leaf	19.163±3.128	8.861±1.695	0.140±0.134	3.005±1.117
Echinops hoelenii	Leaf				
Stachys aculeolata	Total	0.149±0.061	0.109±0.043	0.010±0.010	0.211±0.079
	Leaf	0.063±0.025	0.054±0.024	0.004±0.004	0.105±0.039
Senecio	Leaf	0.044±0.039			
trichopterygius					
Oenanthe procumbens	Leaf				
Solenostemon	Total	11.998±3.827			
sylvaticum	Leaf	4.535±1.330			
Plectranthus spp.	Total	12.612±2.874			
	Leaf	4.555±0.951			
Impatiens spp.	Total	1.405±0.550	0.244±0.173		
	Leaf	0.552±0.223	0.089±0.063		
Vines:					
Droquetia iners	Leaf	0.046±0.027			
Galium spp.		1.994±0.482	0.954±0.129	0.425±0.082	1.341±0.819
Tylophoropsis sp.		0.039±0.039			
Stephania abyssinica		0.041±0.030			
Gynura ruwenzoriensis					
Zehneria scabra					

Appendix 3 (Continued)

Grasses:				
Carex bequaertii				0.290±0.290
Cyperus marii				
Carex simensis	1.723±0.929	2.071±0.902	5.312±1.555	10.657±3.341
Carex erythrorhiza		0.006±0.006	0.493±0.289	20.740±3.475
Carex johnstonii	8.574+4.407	1.806±1.110	1.288±0.977	
Agrostis spp.	0.387±0.156	0.887±0.210	3.000±0.447	3.043±0.598
Poa annua	0.234±0.197	0.003±0.003	0.123±0.105	0.021±0.021
Deschampsia flexuosa				
Festuca schimperiana	0.029±0.024	0.680±0.334	4.438±1.063	3.791±1.612
Festuca engleri	2.602+0.797	22.181±2.759	0.260±0.164	5.137±1.066
Panicum striatissimum			1.043±0.604	
Luzula abyssinica	0.010±0.010	0.456±0.165	1.319+0.327	2.177±0.641
Luzula johnstonii		0.094±0.068	1.212±0.302	0.689±0.279
Mariscus karisimbiensis				
Isolepis spp.			0.753±0.526	0.271±0.170
Juncus dregeanus				
Small herbs:				
Senecio sabinjoensis		0.198±0.078	0.021±0.021	
Helichryssum globosum				
Hydroctyle spp.	3.208±0.532	2.848±0.394	0.815±0.163	4.748±0.486
Parochetus communis	0.282±0.081	0.298±0.082		0.278±0.067
Oxalis				0.035±0.029
Trifolium spp.				
Stelleria sennii	0.492±0.170	0.780±0.254	0.003±0.003	0.560±0.142
Pilea rivularis	0.802±0.241	1.440±0.263	0.017±0.014	0.755±0.256
Alchemilla spp.	0.330±0.096	0.981±0.197	0.250±0.099	1.443±0.401
Alchemilla johnstonii	0.518±0.282	5.456±1.410	12.674±2.503	
Viola emminii	0.439±0.129	0.304±0.097	0.168±0.062	0.634±0.145
Mentha aquatica	0.043±0.027	0.427±0.236		0.014±0.010
Ranunculus spp.	0.029±0.029			0.052±0.023
Cerastium spp.		0.061±0.029	0.014±0.010	0.125±0.058
Hypericum peplidifolium			0.918±0.456	
Cardamine obliqua	0.019±0.019		0.120±0.045	
Rumex bequaertii				
Rumex ruwenzoriense		0.531±0.307		
Geranium arabicum				0.049±0.042
Swertia macrosepala		0.071±0.071	1.349±0.419	0.132±0.132
Polygonum nepalense		0.097±0.079		
Plantago palmata				
Selaginella kraussiana	6.297±1.088	1.159±0.361		1.882±0.970
Total mass	153.223	52.143	31.588	93.956
Total leaf mass	86.955	48.707	29.843	80.282

APPENDIX 4

Equations relating the stem diameter at the point of browsing by an animal (DPB) to the total mass (dry) and leaf mass dry) removed by the animal. The stem diameter was measured across the widest part of the stem where it had been browsed and was measured in centimetres. Mass was measured in grams. The number of samples (n), regression coefficient (r) and significance are given in parentheses.

Species:

Crassocephalum ducis-aprutii:

Total mass: $\text{mass} = 4.78*(\text{DPB})^{2.568}$
(n=37, r=0.82, P<0.001)
Leaf mass: $\text{mass} = 0.74*(\text{DPB})^{0.262}$
(n=37, r=0.83, P<0.001)

Solenostemon sylvaticum:

Total mass: $\text{mass} = 17.37*(\text{DPB})^{3.044}$
(n=42, r=0.87, P<0.001)
Leaf mass: $\text{mass} = (3.739*\text{DPB})^{-0.843}$
(n=43, r=0.85, P<0.001)

Carex bequaertii:

Leaf mass: $\text{mass} = 0.032*(\text{DPB})^{4.686}$
(n=36, r=0.81, P<0.001)

Laportea alatipes:

Total mass: $\text{mass} = 10.43*(\text{DPB})^{2.772}$
(n=43, r=0.95, P<0.001)
Leaf mass : $\text{mass} = 3.33*(\text{DPB})^{2.031}$
(n=43, r=0.87, P<0.001)

Carduus nyassanus:

Total mass: $\text{mass} = 4.72*(\text{DPB})^{1.661}$
(n=27, r=0.84, P<0.001)
Leaf mass: $\text{mass} = 1.63*(\text{DPB})^{2.582}$
(n=26, r=0.87, P<0.001)

Impatiens spp.:

Total mass: $\text{mass} = 5.03*(\text{DPB})^{2.711}$
(n=49, r=0.91, P<0.001)
Leaf mass: $\text{mass} = 1.02*(\text{DPB})^{2.082}$
(n=49, r=0.89, P<0.001)

Peucedanum linderi:

Stem mass: $\text{mass} = 16.58*(\text{DPB})^{1.198}$
(n=29, r=0.75, P<0.001)
Leaf mass: $\text{mass} = 4.59*(\text{DPB})^{2.962}$
(n=43, r=0.91, P<0.001)

APPENDIX 5

Fitted curves through the relative growth rates ($gg^{-1}d^{-1}$) measured for plants of varying mass. Curves are of the form: *Growth rate* = Ae^{B*mass} and the values of *A*, *B* and the number of samples (n), and significance of fit are given in the table. Growth rates were measured for both the total plant mass and for the leaf mass increase per unit mass and for stem increase for thistles and the wild celery.

		A	*B*	n	P<
Crassocephalum ducis-aprutii	Total	0.011	-0.043	103	0.001
	Leaf	0.010	-0.325	103	0.001
Laportea alatipes	Total	0.010	-0.052	133	0.001
	Leaf	0.012	-0.750	131	0.001
Urtica massaica	Total	0.028	-0.097	110	0.001
	Leaf	0.031	-0.370	110	0.001
Solenostemon sylvaticum	Total	0.007	-0.494	80	0.001
	Leaf	0.008	-1.660	81	0.001
***Impatiens* spp.**	Total	0.010	-0.341	75	0.001
	Leaf	0.010	-2.150	74	0.001
Peucedanum linderi	Stem	0.009	-0.104	83	0.001
Carduus nyassanus	Stem	0.059	-0.102	31	0.001

The leaf growth rates of *Carduus nyassanus* were linear rather than exponential:

$$Growth\ rate = 4.6\times10^{-3} - 3.3\times10^{-4} mass$$

The leaf growth rates of *Peucedanum linderi* were very variable and showed no pattern. The mean of these values was taken as the growth rate.